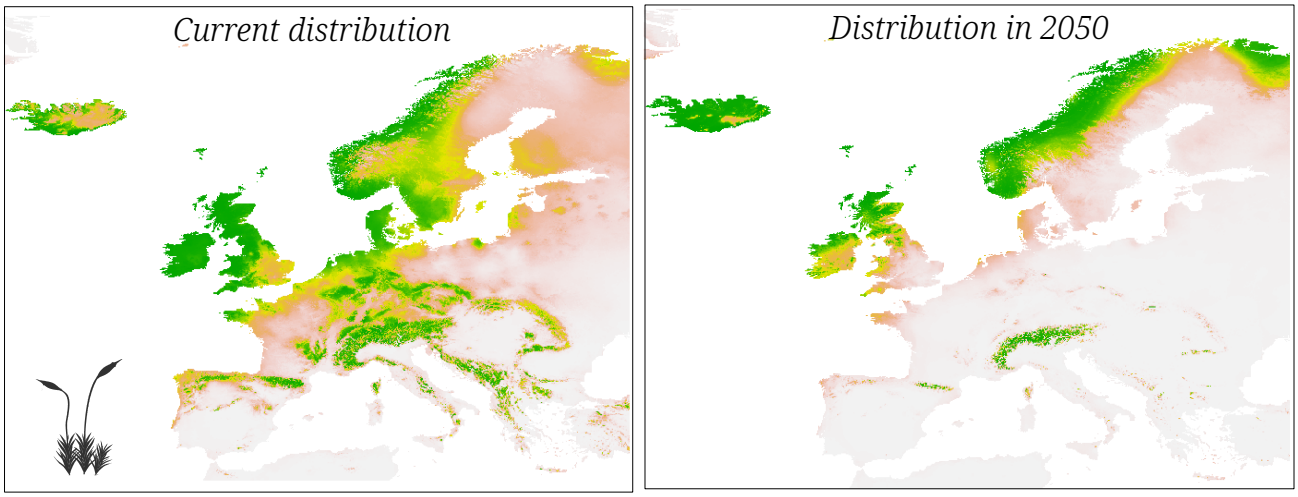
Predicting the dynamics of range shifts under climate change: assumptions and applications to the European bryophyte flora



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Predicting the dynamics of range shifts under climate change: assumptions and applications to the European bryophyte flora

Thesis submitted in fulfilment of the requirements for the degree of Doctor in Sciences

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Cover picture derived from the study presented in chapter III. Possible distributions of a moss at present-time and in 2050.

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Abstract

Climate change has and will have a dramatic impact on species ranges. Terrestrial species have accordingly already migrated poleward at a median speed of 16.9km per decade since the beginning of the industrial era. However, many species are not equipped to efficiently track the geographic changes of the conditions matching their climatic niche, and are consequently prone to extinction. No less than about 20% of land plant species are hence threatened with extinction in the future, with major consequences on human food resources and health. In this context, Species distribution models (SDMs) offer an appealing framework to test the potential effects of climate change on species ranges. Like many biodiversity analyses, SDMs have traditionally been conducted at the species level. Cryptic speciation, which results in taxa that cannot rapidly be distinguished morphologically, but underwent divergent evolutionary histories, has been, however, increasingly reported, raising the question of whether SDMs should be fitted at the level of species (clade models), cryptic species or intraspecific lineages (subclade models). Projecting models through time further raises several questions and relies on several assumptions. In particular, projecting species potential ranges in the future based on their niche inferred from extant climate conditions onto future climatic layers involves that (I) species climatic niches are conserved through time (niche conservatism hypothesis) and that (ii) species are at equilibrium with their environment (i.e. their entire niche is filed), implying that they are not limited by their dispersal capacities, and are immediately able to colonize any newly suitable area.

Focusing on bryophytes, whose ecophysiological characteristics, such as poikilohydry and reliance on rainfall for water uptake, make them excellent candidates to study the impact of climate change, but which exhibit reduced morphologies, raising concerns about broadly defined morphological species concepts, we address here the following questions:

1 At which taxonomic level should SDMs be computed? We compare the extent to which model projections generated at the level of species differ from those obtained for intraspecific lineages. Modelling at the level of infraspecific lineages raises a second issue, which is associated with the very small sample sizes that typically characterize molecularly defined lineages, that is: how can ensemble of small models calibrated from very small datasets be evaluated? In the light of analyses of niche overlap, we finally determine whether models should be calibrated at the level of the species or intraspecific lineages.

2 Is there climatic niche conservatism in bryophytes, and how does the tendency for closely related taxa to share the same climatic niche vary at increasing taxonomic depth?

3 To what extent will such efficient dispersers as bryophytes successfully track the shift of their suitable areas during the next decades?

To address Q1, Ensembles of Small Models were evaluated by null models calibrated from randomly sampled presence points. We compared the extent of suitable area predicted by the projections of clade and subclade models. Niche overlaps were quantified using Schoener's D and Hellinger's I metrics, and the significance of these metrics in terms of niche conservatism or divergence was assessed by niche similarity tests. Combined predictions from subclade models contributed, on average, five times more than clade models to the total suitable area predicted by the combination of both subclade and clade models. Niche overlap was 0.71 on average, with evidence for niche conservatism in half of the species and no signal for niche divergence. Given the poor performance of models based on small datasets, we pragmatically suggest

that, in the absence of evidence for niche divergence during diversification of closely related intraspecific lineages, SDMs should be based on all available occurrence data at the species level.

The hypothesis of climatic niche conservatism and its evolutionary 'labillity' was further tested at the level of an entire phylum of land plants, the Marchantiophyta, through analyses of the relationship between the spatial turnover of floras and macroclimatic variation. Phylogenetic turnover among floras was quantified through π_{st} statistics. π_{st}-through-time profiles were generated at 1 myr intervals along the phylogenetic time-scale and were correlated with current geographic distance and macroclimatic variation with Mantel tests based on Moran spectral randomization to control for spatial autocorrelation. The contribution of macroclimatic variation to phylogenetic turnover was about four-times higher than that of geographic distance. The correlation between phylogenetic turnover and geographic distance rapidly decayed at increasing phylogenetic depth, whereas the relationship with macroclimatic variation remained constant until 100 myrs. Our analyses reveal that changes in the phylogenetic composition among liverwort floras across the globe are primarily shaped by macroclimatic variation. They demonstrate the relevance of macroclimatic niche conservatism for the assembly of liverwort floras over very large spatial and evolutionary time scales, which may explain why such a pervasive biodiversity pattern as the increase of species richness towards the tropics also applies to organisms with high dispersal capacities.

Finally, we developed a newly designed spatially-explicit model of dispersal by wind in the context of changing climate and presented an example of application in the case of the European flora. A grid of pixel-specific environmental conditions and dispersal kernels, combining information on species dispersal traits, local wind conditions, as well as landscape features affecting dispersal by wind, was generated and used as input in simulations of species dispersal in the landscape under changing climate conditions. In European bryophytes, the median ratios between predicted range loss vs expansion by 2050 across species and climate change scenarios ranged from 1.6 to 3.3 when only shifts in climatic suitability were considered, but increased to 34.7–96.8 when species dispersal abilities were added to our models. This highlights the importance of accounting for dispersal restrictions when projecting future distribution ranges and suggests that even highly dispersive organisms like bryophytes are not equipped to fully track the rates of ongoing climate change in the course of the next decades.

Résumé

Les changements climatiques ont et auront un impact important sur la distribution des espèces. En effet, les espèces terrestres ont déjà migré vers les pôles à une vitesse médiane de 16.9km par décennie depuis le début de l'ère industrielle. Cependant, de nombreux taxa semblent ne pas être capables de suivre le déplacement de leur aire climatiquement favorable et sont donc voués à disparaître. Pas moins de 20% des plantes terrestres sont ainsi menacées d'extinction dans le futur, avec d'importantes conséquences pour la santé et l'alimentation humaine. Dans ce contexte, les modèles de distribution d'espèces (SDMs) apparaissent comme de puissants outils pour tester l'impact potentiel des changements climatiques sur la distribution des espèces. Comme beaucoup d'analyses sur la biodiversité, les SDMs ont traditionnellement été appliqués au niveau de l'espèce. Or, la prise de conscience croissante que les espèces cryptiques représentent une grande partie de la biodiversité soulève la question du niveau taxonomique auquel les SDMs devraient être conduits. En outre, de nombreuses questions émergent lorsque les SDMs sont projetés dans le temps. Plus particulièrement, lorsqu'on projette la niche d'une espèce sur des couches climatiques futures pour prédire sa répartition potentielle, on suppose que l'espèce (i) conserve sa niche dans le temps (conservatisme de niche) et (ii) est en équilibre avec son environnement, impliquant que les capacités dispersives de l'espèce ne sont pas limitées, et que l'espèce colonise immédiatement toutes les nouvelles zones viables.

Pour cette thèse, nous nous sommes intéressés aux bryophytes, qui sont d'excellents candidats pour étudier l'impact des changements climatiques grâce à leurs caractéristiques écophysiologiques, en particulier leur poïkilohydrie et leur dépendance aux précipitations atmosphériques pour l'alimentation hydrique. Par ailleurs, la question du rang taxonomique au niveau duquel les SDMs doivent être conduits est particulièrement critique chez les bryophytes en raison de leur morphologie réduite et de l'importance de la spéciation cryptique dans le groupe. Dans ce contexte, nous avons abordé les questions suivantes:

1 À quel niveau taxonomique les SDMs devraient-ils être appliqués ? Nous avons comparé l'étendue des aires climatiquement favorables obtenues en générant des modèles au niveau de l'espèce et au niveau de lignées intraspécifiques. Modéliser au niveau intraspécifique soulève cependant une série de problèmes relatifs au faible nombre d'occurrences disponibles dans des lignées que l'on ne peut caractériser que d'un point de vue moléculaire, notamment l'évaluation des modèles calibrés sur des effectifs réduits.
2 Y a-t-il conservatisme de niche chez les bryophytes ? Dans quelle mesure ce conservatisme se rencontre-t-il toujours dans des lignées de rangs taxonomiques supérieurs ?
3 Dans quelle mesure les bryophytes, qui présentent de grandes aptitudes à la dispersion, réussiront-elles à suivre le déplacement spatial de leurs aires climatiquement favorables en réponse au réchauffement climatique dans les prochaines décennies ?

Pour répondre à la première question, les assemblages de petits modèles (ESMs) ont été évalués via des modèles nuls calibrés à partir d'occurrences aléatoirement choisies dans la zone d'étude. Ces ESMs ont été utilisés pour comparer l'étendue des aires climatiquement favorables obtenues à partir de modèles produits au niveau de l'espèce et de lignées intraspécifiques. Le degré de recouvrement des niches aux différents niveaux taxonomiques a été quantifié avec les métriques D de Schoener et I d'Hellinger et l'hypothèse du conservatisme ou de la divergence de niche testée avec des tests de similarité. Le rang taxonomique s'est révélé avoir une importance considérable sur l'évaluation de l'étendue de l'aire climatiquement favorable. En effet, la combinaison de modèles construits au niveau des lignées intraspécifiques d'une espèce a conduit à des aires climatiquement favorables en moyenne cinq fois plus grandes que les aires estimées à partir d'un modèle construit au niveau de l'espèce entière. Le degré de recouvrement des niches entre lignées intraspécifiques était de 0,71 en moyenne. Les tests de similarité ont révélé que, chez la moitié des

espèces étudiées, il y avait conservatisme de niche entre les lignées intraspécifiques. Aucun signal de divergence de niche n'a été mis en évidence. Dès lors, et au vu de la faible performance des modèles basés sur les petits jeux de données, nous suggérons qu'en l'absence de divergence de niche entre deux lignées intraspécifiques, les SDMs devraient être basés sur toutes les données d'occurrences possibles au niveau de l'espèce.

L'hypothèse du conservatisme de niche a également été testée au travers d'analyses de la relation entre le turnover phylogénétique et les facteurs environnementaux à différents niveaux phylogénétiques au sein d'un phylum entier de plantes terrestres, les hépatiques. Le turnover phylogénétique entre les flores d'hépatiques a été quantifié avec la métrique π_{st} et a été corrélé avec les distances géographiques et les variations macroclimatiques avec des tests de Mantel basés sur une randomisation du spectre de Moran afin de contrôler l'auto-corrélation spatiale. La contribution des variations macroclimatiques sur le turnover phylogénétique était quatre fois supérieures à celle des distances géographiques. L'analyse de ces corrélations à des rangs taxonomiques croissants a révélé que la corrélation entre le turnover phylogénétique et les distances géographiques diminue très rapidement à haut niveau taxonomique. *A contrario*, la corrélation entre π_{st} et les variations macroclimatiques est restée quasiment constante jusqu'à 100 millions d'années. Nos analyses révèlent que les changements dans la structure phylogénétique des flores d'hépatiques résultent principalement des variations macroclimatiques et démontrent l'importance du conservatisme de niche macroclimatique sur l'assemblage des flores d'hépatiques à travers de très grandes échelles spatiales et temporelles. Ces résultats peuvent expliquer pourquoi une loi aussi universelle en écologie que le gradient latitudinal de biodiversité s'applique également à des organismes aussi dispersifs que les hépatiques.

Enfin, nous avons créé un modèle spatialement explicite de dispersion par le vent dans le contexte des changements climatiques et nous avons présenté un exemple d'application sur la flore bryophytique européenne. Pour ce faire, nous avons généré des grilles de conditions climatiques et de kernels de dispersion, combinant des informations spécifiques telles que la taille des spores, des données de vents ainsi que des caractéristiques du terrain affectant la dispersion par le vent. Nous avons utilisé ces inputs pour réaliser des simulations de dispersion sous la contrainte des changements climatiques. Cette approche nous a permis d'évaluer l'impact des changements climatiques sur un groupe anémochore de bryophytes en prenant en compte les variations locales de préférence de niche et les limites dispersives à une échelle continentale. Les ratios médians entre la perte et le gain d'aires climatiquement favorables en 2050 pour chaque espèce et selon différents scénarios du futur étaient compris entre 1,6 et 3,3 lorsque l'on prenait seulement le climat en compte et augmentaient jusqu'à 34,7-96,8 quand les limites dispersives étaient ajoutées aux modèles. Ces résultats montrent l'importance d'intégrer les limites dispersives des espèces quand on fait des prédictions sur leurs aires de répartition futures et suggèrent que même des espèces très dispersives telles que les bryophytes ne sont pas capables de suivre totalement la cadence des changements climatiques au cours des prochaines décennies.

List of contributions

The thesis is based on the following articles:

I. **Collart, F.**, Hedenäs, L., Broennimann, O., Guisan*, A., Vanderpoorten*, A. 2021. Intraspecific differentiation: Implications for niche and distribution modelling. *Journal of Biogeography*. 48, 415–426. https://doi.org/10.1111/jbi.14009

II. **Collart*, F.**, Wang*, J., Patiño*, J., Hagborg, A., Söderström, Goffinet, B., Magain, N., Hardy*, O.J., Vanderpoorten*, A. Macroclimatic structuring of spatial phylogenetic turnover in liverworts. *Manuscript accepted with minor revision in Ecography*.

III. Zanatta*, F., Engler*, R., **Collart*, F.**, Broennimann, O., Mateo, R.G., Papp, B., Muñoz, J., Baurain, D., Guisan*, A., Vanderpoorten*, A. 2020. Bryophytes are predicted to lag behind future climate change despite their high dispersal capacities. *Nature Communications*. 11, 1–9. https://doi.org/10.1038/s41467-020-19410-8

* These authors contributed equally to the study

and the contribution of the following article (in appendix):

IV. Mouton, L., Patiño, J., Carine, M., Rumsey, F., Menezes de Sequeira, M., González-Mancebo, J.M., Gabriel, R., Hardy, O.J., **Collart, F.**, Vanderpoorten, A. Variation of Beta diversity across geographic scales and taxonomic groups in the Macaronesian land plant flora. *Manuscript*

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1. General introduction

The Anthropocene has been recently described as a new geologic era to mark the deep environmental impact of human activities (Subramanian, 2019). When the period actually started remains, however, hotly debated (Lewis and Maslin, 2015), and several competing dates have been proposed, including the earliest detectable human impacts; the 17th century, a period characterized by massive movements of species, atmospheric CO2 decline and resulting climate-related changes (Zalasiewicz, 2015); and 1960, which corresponds to the start of the Great Acceleration (Steffen et al., 2015), a period of major expansion in human population, large changes in natural processes, and the development of novel materials. If the actual definition of the Anthropocene thus still remains controversial, it nonetheless remains that the idea of the recognition of a new geological period characterized by a boom of human activities and its environmental consequences is widely accepted today (Zalasiewicz, 2015).

In this context, the last report of the Intergovernmental Panel on Climate Change (IPCC) points to an increase of approximately 1°C compared to the pre-industrial era, corresponding to an average warming of 0.2°C per decade due to human activities (Fig.1). If additional governmental measures are not taken to reduce greenhouse gases, the temperature increase will be of 1.5°C around 2040 (Allen et al., 2018).

Whether species will have the capacities to track the spatial shift of their suitable habitats (i.e. where conditions match their niche) under climate change has been one of the major questions during the last decades (Pecl et al., 2017). To determine the speed at which species need to disperse to spatially track suitable conditions under climate change, the velocity of climate change was introduced as the instantaneous local velocity along Earth's surface needed to maintain constant temperatures (Hamann et al., 2015; Loarie et al., 2009; Molinos et al., 2019), representing the needed moving speed for a species to keep pace spatially with its suitable climatic conditions under climate change (Brito-Morales et al., 2018). Worldwide, the velocity for mean annual temperature between 1975 and 2013 was 11km on average per decade (Ordonez et al., 2016). In comparison, the climate change velocity between the last glacial maximum and the present time was on average 594m per decade (Sandel et al., 2011), with potentially higher or lower rates during certain time periods (Corlett and Westcott, 2013; Garcia et al., 2014; Heikkinen et al., 2020; Molinos et al., 2016; Saladin et al., 2020; Vanderwal et al., 2013). The climate change velocities predicted for the next 65 years are thus 40 to 3000 times higher than those observed since the last glacial maximum (Sandel et al., 2017). In response to climate change, terrestrial species have migrated poleward at a median speed of 16.9km per decade and at higher elevations at a median speed of 11m per decade since the beginning of the industrial era (computed from data comprised between 1880 and 2007) (Chen et al., 2011; Pecl et al., 2017), whereas distributions of marine species have moved toward the pole by 72km on average (data comprised between 1990 and 2010) (Poloczanska et al., 2013). However, many species are not equipped to efficiently track their climatic niches, and are consequently prone to extinction (Dullinger et al., 2012; Parmesan, 2006; Rumpf et al., 2019; Wiens, 2016).

Human-induced climate change, habitat fragmentation, pollution, overfishing and overhunting have resulted in initiating what might become the Earth's sixth mass extinction (Barnosky et al., 2011; Ceballos et al., 2017, 2015; McCallum, 2021; Pimm et al., 2014; Torres-Romero et al., 2020). 25% of animal and plant species are impacted by human activities, with an estimate of one million species being already at risk of extinction (IPBES, 2019). For example, the number of vertebrates that have already disappeared since 1900 is 543 and this number is predicted to double in 2050, leading to an extinction rate in 2050 that is 117 times higher than the background rate (computed from the last two million years and representing 2 species loss

per century for every 10,000 species; Ceballos et al., 2020). In addition, ~20% of the total land plant species, and more specifically, 50,000 of the ~390,000 vascular plant species are predicted to become extinct in the future (Brummitt et al., 2015; Cronk, 2016; Humphreys et al., 2019). This is especially true in biodiversity hotspots (Le Roux et al., 2019) such as Amazonia where an extinction rate up to 58% of tree species is predicted in 2050 (Gomes et al., 2019). The associated biodiversity loss is expected to impact ecosystem functioning and services, and hence, to have an impact on food resources such as crop yields and fisheries, and health (Schmeller et al., 2020; Cardinale et al., 2012; Johnson et al., 2017; Roe, 2019; Roe et al., 2019).

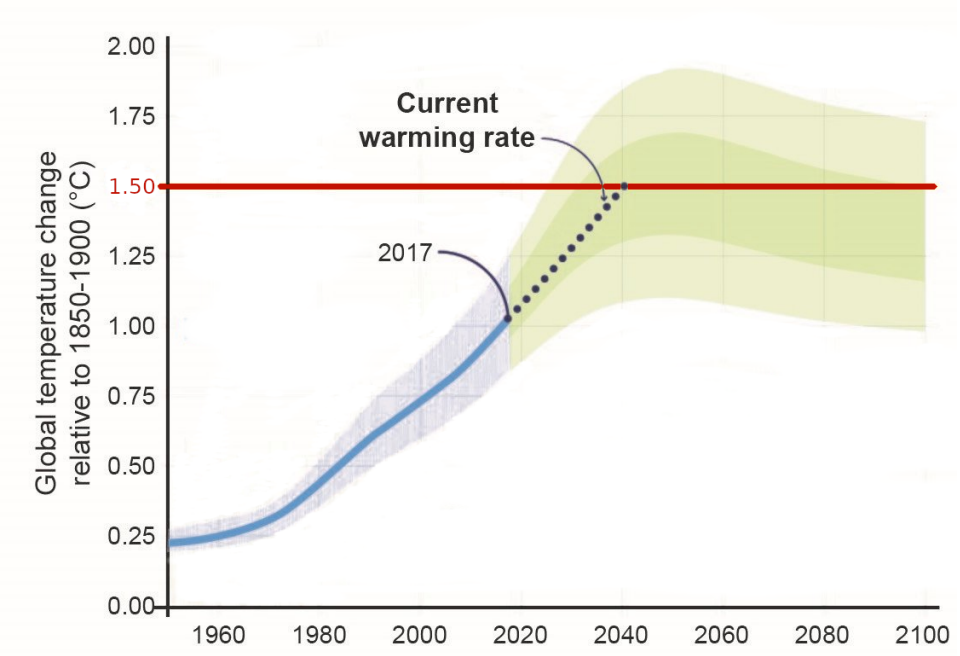

Fig.1. Global temperature change relative to the pre-industrial temperatures (1850-1900). The blue line corresponds to observed warming. The black dot line is the predicted temperature increase if the same trend applies during the next decades. The green ribbon represents the tendencies if CO2 emissions decrease; the lower bound represents the expected temperature range if CO_2 emissions reach 0 (Modified from Allen et al., 2018).

In the context of climate change, species distribution models (SDMs), also called ecological niche models (ENMs), habitat suitability models (HSMs) or other names (Box 1; see also Guisan et al., 2013), offer an appealing framework to test the potential effects of climate change on species ranges (Araújo et al., 2019; Guisan et al., 2017; Pacifici et al., 2015; Taheri et al., 2021).

SDMs are typically projected onto different areas, or different time periods, to predict, for instance, the potential of spread of invasive species in their introduced range (Barbet-Massin et al., 2018; Bertolino et al., 2020; Briscoe Runquist et al., 2021; Dinis et al., 2020; Vicente et al., 2013), or the predicted distribution of species in the past or the future (Avendaño-González and Siqueiros-Delgado, 2021; Biber et al., 2020; Dagtekin et al., 2020; Della Rocca and Milanesi, 2020; Nascimbene et al., 2020). Projecting models trough time or space raises, however, several questions and relies on several assumptions (Wiens et al., 2009; Zurell et al., 2020a).

Box1 – Species Distribution Models: How do they work?

Species Distribution Models (SDMs) are powerful research tools based on the concept of ecological niche (Hutchinson, 1957; Soberón, 2007) and applied to various scientific fields such as ecology, evolution and conservation (Boulangeat et al., 2014; Broennimann et al., 2014; Guisan et al., 2013; Johnson et al., 2019; Ramel et al., 2020; Vincent et al., 2019). SDMs allow to infer the drivers of biodiversity as a function of the spatial scale (Guisan and Zimmermann, 2000; Honrado et al., 2016; Merow et al., 2014) but to also predict spatial species distributions in response to diverse modification of their environment caused by climate change (Braz et al., 2019; Kling and Ackerly, 2020; Pang et al., 2021; Schickele et al., 2021), land-use (Barras et al., 2021; Hülber et al., 2020; Ramachandran et al., 2018) and invasive species (Cucco et al., 2021; Gallardo et al., 2017; Lake et al., 2020; McMahon et al., 2021; Vicente et al., 2013). SDMs are widely used nowadays, notably due to the emergence of websites sharing species occurrence data (e.g. gbif.org) and worldwide environmental databases at large and fine scale (~1km of resolution; Fick and Hijmans, 2017; Karger et al., 2017), but also due to the development of versatile softwares such as Maxent (Phillips et al., n.d.) or R packages such as biomod2 (Thuiller et al., 2009, 2019a), ecospat (Broennimann et al., 2017; Di Cola et al., 2017) and sdm (Naimi and Araújo, 2016).

The methodology of SDMs can be split into three parts (see Fig. A; Guisan and Zimmermann, 2000; Guisan et al., 2017). First, it is important to acquire species and environmental data. Species data can be presences/absences, only presences or abundances (Elith and Leathwick, 2009), which can be obtained from field work, herbarium or museum records and websites (Guisan et al., 2017; Guisan and Thuiller, 2005). The environmental data are usually spatial grids with a given resolution generated from meteorological stations (Fick and Hijmans, 2017; Karger et al., 2017; Randin et al., 2006), satellite data ("CORINE Land Cover — Copernicus Land Monitoring Service," 2021; Danielson and Gesch, 2011; Wüest et al., 2020; Yamazaki et al., 2017) or soil sampling (Buri et al., 2017; Hengl et al., 2017; Stoorvogel et al., 2017). It is important to carefully choose which environmental variables are important for the studied species (Austin and Van Niel, 2011; Fourcade et al., 2018; Petitpierre et al., 2017), and to select sets of variables with low correlations between them in order to avoid multicollinearity issues (Dormann et al., 2013; Zurell et al., 2020a).

After generating a species occurrence data set and selecting the most important environmental variables, species ecological niches can be modeled via species response curves allowing to link species observations to their environment (Guisan et al., 2017). To do so, several modeling techniques have been developed, including envelopes (e.g. Ecological-Niche Factor Analysis [ENFA; Hirzel et al., 2002] and HABITAT (Walker and Cocks, 1991)), regression-based methods (e.g. General Linear Models [GLM; Nelder and Wedderburn, 1972] and General additive models [GAM; Hastie and Tibshirani, 1986 but see Guisan et al., 2002]), classification (e.g. by boosting: Gradient Boosting Machine [GBMs; Elith et al., 2008; Friedman, 2001] and bagging: Random Forest [RF; Breiman, 2001, 1996; Ho, 1995]), artificial intelligence (Artificial neural networks; Ripley, 1996; Venables and Ripley, 2002) and maximum entropy (MAXENT; Phillips et al., 2017, 2006, 2004). All these techniques rely on different assumptions and exhibit contrasting performances. To take model uncertainty into account and improve the predictive power, it is recommended to use several modeling techniques and make a consensus model (Araújo and New, 2007; Hao et al., 2019; Thuiller et al., 2019b).

Following calibration, models need to be evaluated. To this aim, several metrics for presence-absence data have been developed, such as the "Area Under the Curve" (AUC; Fielding and Bell, 1997), the True Skill Statistic (TSS; Allouche et al., 2006) or Cohen's kappa (Cohen, 1960), and some metrics for presence-only data, such as the Boyce index (Hirzel et al., 2006).

The last part of the modeling process is to project ecological niches onto a geographical environment. Ecological niches can be projected at different time scales in the future (Biber et al., 2020; Della Rocca and Milanesi, 2020; Reside et al., 2019) or in the past (Colli-Silva et al., 2021; Napier et al., 2020), but can also be projected onto different geographic areas, to study, in particular, the potential range of invasive species

(Barbet-Massin et al., 2018; Briscoe Runquist et al., 2021).

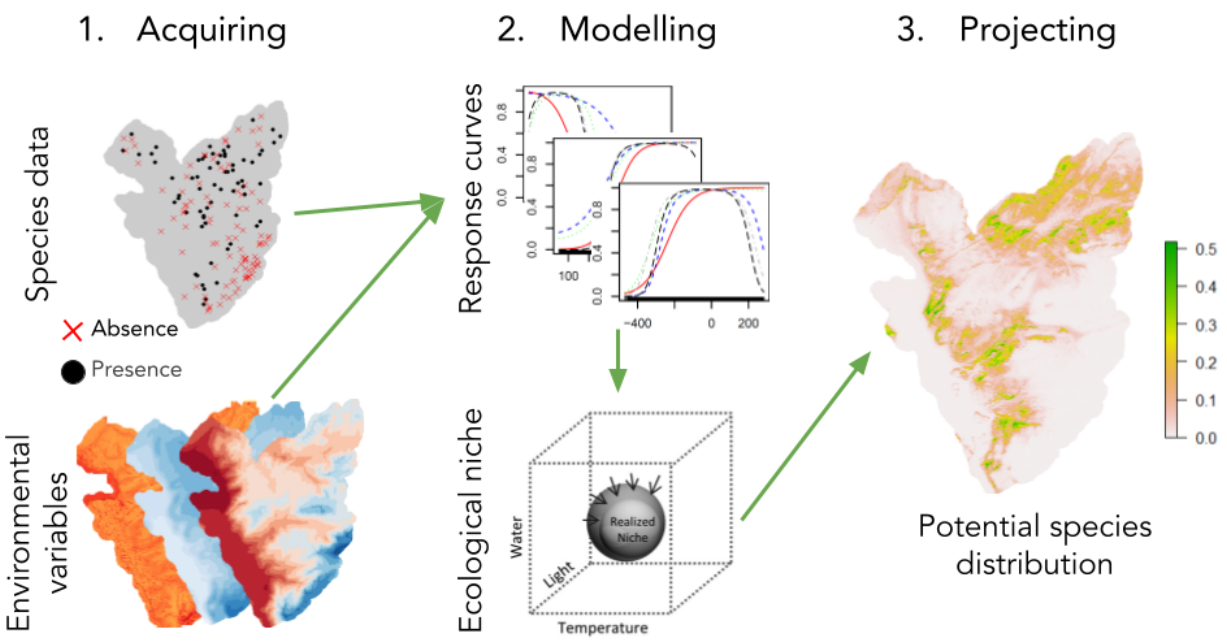

Fig. A: Overview of a standard methodology to model species distributions with an example of a fictive species in Canton of Vaud (Switzerland) (adapted from Guisan et al., 2017). The first step is to acquire species observations (presences or absences) and environmental data. Then, the two types of data are statistically linked to generate response curves. These curves allow to model the ecological niche of the species. Afterwards, this niche is projected onto a geographical space to represent the potential distribution of the studied species.

1.1. At which taxonomic level should SDMs be conducted?

Like many biodiversity analyses, SDMs have traditionally been conducted at the species level (hereafter clade models; Pearman et al., 2010). Cryptic species, i.e., taxa that cannot readily be distinguished morphologically, but underwent divergent evolutionary histories, and which occur on all major branches of the tree of life where they probably represent a significant portion of undiscovered biodiversity, have been, however, increasingly reported (Jörger and Schrödl, 2013; Struck et al., 2018). Mounting evidence for cryptic speciation thus raises the question of whether species distribution models should be conducted at the species level, cryptic species or intraspecific lineages (hereafter subclade models; Pearman et al., 2010; Smith et al., 2019). The niche conservatism hypothesis predicts low niche differentiation between species over evolutionary time scales (Peterson, 2011; Peterson et al., 1999; Wiens, 2004; Wiens and Graham, 2005). The role of local adaptation in species diversification has, however, been increasingly acknowledged (Chardon et al., 2019; Peterson et al., 2019; Platania et al., 2020; Poulin and Pérez-Ponce de León, 2017; Sork, 2017), with major consequences for our ability to accurately infer species niches.

Cryptic species and intraspecific lineages are typically characterized by molecular data to identify which specimens belong to a given lineage. As a result, the number of available occurrences for cryptic species is

much smaller than that for long-recognized species, whose distributions are widely documented in databases such as GBIF (gbif.org). The comparatively small number of actual observations at the intraspecific level or for cryptic species raises issues related to sample size for both model calibration and evaluation (Maguire et al., 2018). To address these issues, Ensembles of Small Models (ESMs) have been developed to calibrate models from small datasets (Breiner et al., 2018, 2015; Lomba et al., 2010). ESMs compute models generated with a very small number of explanatory variables at a time (i.e., 'small models', typically two predictors at a time), and then combine them by averaging all of these small models into an ensemble, in a similar way as done for multi-techniques ensemble forecasting (Araujo & New 2007, Thuiller et al. 2009). With this procedure, ESMs circumvent the overfitting issue without reducing the explanatory power. ESMs applied to rare species significantly perform better than normal SDMs (Breiner et al., 2015). However, model evaluation based on a small number of occurrences still remains problematic (Jiménez-Valverde, 2020). For ESMs, Breiner et al. (2015, 2018) recommended to compute accuracy values such as AUC and TSS by keeping a proportion of the data for model calibration and using the remaining of the data for evaluation, replicating this operation n times, and then averaging the values of the statistics across replicates. For a data set with 10 presences and keeping 20% of hold-out data for calibration, this would leave as few as 2 points per replicate for model evaluation, whereas Jiménez-Valverde (2020) most recently recommended that minimum sample sizes of 20 (10 presences and 10 true absences) should be used when attempting at evaluating models through bootstrapping.

1.2. Species distribution models and the niche conservatism hypothesis

Model projections are only valid if species niches are constant in time and space (Guisan et al., 2017; Wiens et al., 2009; Zurell et al., 2020a). The niche conservatism hypothesis precisely posits that species niches are evolutionary constrained (Peterson, 2011; Peterson et al., 1999; Wiens, 2004; Wiens et al., 2010; Wiens and Graham, 2005), which involves that niche preferences remain constant through space and time (Bush et al., 2016; Pearman et al., 2008; Petitpierre et al., 2012; Randin et al., 2006). The tendency of species to retain their niches and related ecological traits over time (Wiens et al., 2010) has emerged as one of the most important principles in ecology and evolution for explaining patterns of species richness and phylogenetic relatedness at different spatial and temporal scales (Araújo and Peterson, 2012; Peterson, 2011; Pyron et al., 2015; Wiens, 2004; Wiens and Donoghue, 2004). The role of local adaptation in species diversification has, however, been increasingly acknowledged (Bocedi et al., 2013; Chardon et al., 2019; Peterson et al., 2019; Sork, 2017), challenging the niche conservatism hypothesis (Broennimann et al., 2007; Cardador and Blackburn, 2020; Guisan et al., 2014; Jezkova et al., 2011; Pili et al., 2020; Sherpa et al., 2019; Srivastava et al., 2020; Wiens et al., 2019). Rejection of the latter has important consequences when one attempts at projecting models in space and time. This is typically the case in invasion biology, wherein one of the most important questions is to identify which areas are the most sensitive to biological invasions from models calibrated in the area of origin of alien species (Broennimann et al., 2007; Petitpierre et al., 2012). Another timely example involves the projection of model calibrated from extant species distributions and climate conditions onto future climatic layers in the context of climate change (Hällfors et al., 2016; Maguire et al., 2018; Pearman et al., 2010; Valladares et al., 2014; Yannic et al., 2014).

Testing niche conservatism is therefore of utmost importance for modelling. This can be done via several methods, which can be divided into two categories based on the analysis of phylogenetic structure (Crisp and Cook, 2012) and of species niche preferences (Broennimann et al., 2012; Warren et al., 2008). Phylogenetically-based methods typically aim at assessing the 'heritability' of niche traits through the computation of the phylogenetic signal in those traits by means of metrics such as Moran's I (Gittleman and Kot, 1990; Moran, 1950), Pagel's λ (Freckleton et al., 2002; Pagel, 1999), or the δstatistic (Borges et al., 2019; Diniz-Filho et al., 2012; Molina-Venegas and Rodríguez, 2017; Münkemüller et al., 2012). Whether significant phylogenetic signal in a niche trait evidences niche conservatism has, however, been questioned (Losos, 2008; Münkemüller et al., 2015). Alternatively, phylogenetic niche conservatism can be tested at the level of communities by measuring the phylogenetic turnover among communities(Π_{st}) (Hardy and Senterre, 2007; Parmentier and Hardy, 2009; Hardy, 2008; Vamosi et al., 2009). Phylogenetic turnover compares the average phylogenetic distances among species within and between communities (Graham and Fine, 2008) and is influenced by two main macroecological and evolutionary drivers: habitat specialization and dispersal limitations (Hardy et al., 2012; Saladin et al., 2019; Segovia et al., 2020). The niche conservatism hypothesis posits that species sharing the same niche should, on average, be more phylogenetically related to each other than pairs of species from different niches, creating significantly higher phylogenetic turnover between than within habitats (Graham and Fine 2008, Segovia et al. 2020). Therefore, phylogenetic niche conservatism can be detected when the distribution of ecological traits matches both species distributions and evolutionary relationships (Losos 2008), i.e., when phylogenetic turnover and environmental variation are significantly correlated (Fig. 2) (Jin et al. 2015; Hardy et al., 2012).

Methods based on the analysis of species niche preferences for inferring niche conservatism rely on the evaluation of niche overlap among taxa. For instance, one can compute the ability of a taxon to predict the distribution of another, phylogenetic-close taxon (Peterson et al., 1999; Peterson and Holt, 2003). Another option is to compare the niche overlap estimates derived from the observed niche with random niche overlaps that would be expected by chance (Broennimann et al., 2012; Stockman et al., 2008; Warren et al., 2008).

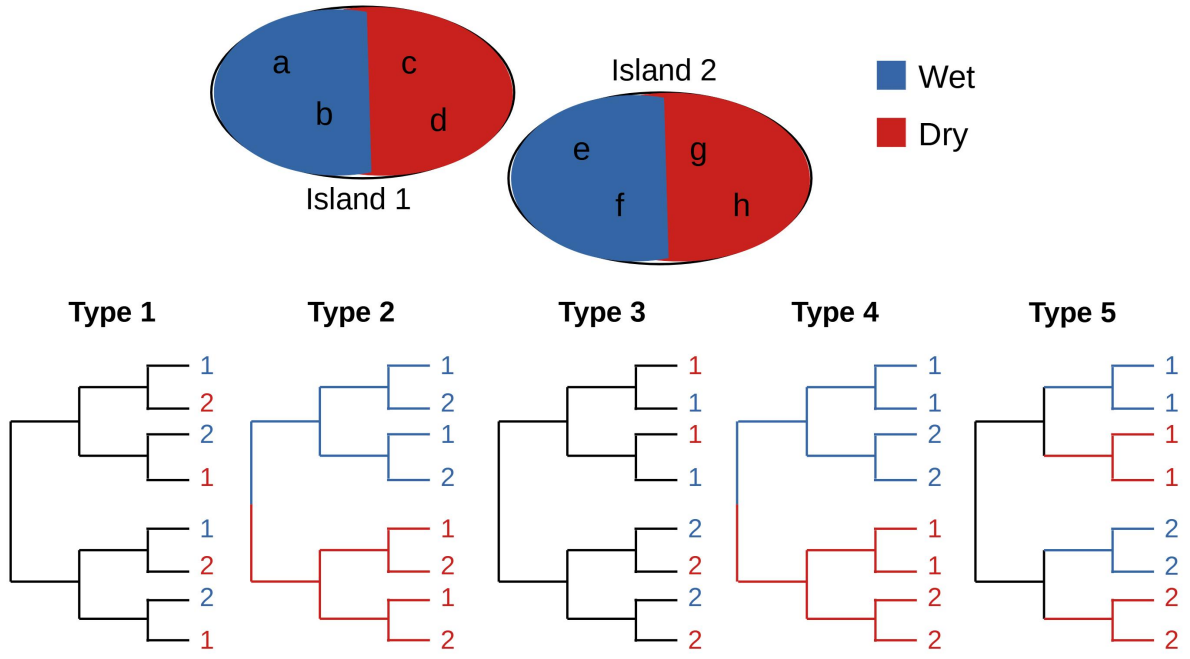

Fig. 2: Hypothetical patterns of phylogenetic turnover exploring different combinations of geographical (two islands 1 and 2) and ecological (two habitats, wet (in blue) and dry (in red)) structure (redrawn from Graham & Fine, 2008). The five phylogenies show various degrees of niche conservatism and dispersal imitations. Type 1 corresponds to a situation where species phylogenetic clustering cannot be interpreted in terms of geographic nor ecological factors. Type 2 is structured by habitat and only involves niche conservatism. Type 3 is structured by geography but not niche preference. Type 4 is primarily arranged by habitat and secondarily by geography while type 5 exhibits the reverse pattern.

1.3. Species distribution models and dispersal

SDMs have often been used to assess species potential ranges by projecting their modelled niches. Whether species occupy their entire suitable niche, and are hence at equilibrium with their environment (Araújo and Pearson, 2005), or have not yet colonized their potential distribution area, largely depends on their dispersal capacities. For example, Svenning et al. (2008a) evidenced that the extent of the mismatch between the observed and predicted range of European tree species can be explained in terms of the speed at which these species were successful in recolonizing northern areas since the Last Glacial Maximum. In this context, projecting species niches onto future climatic layers to infer the impact of climate change on species distributions has been increasingly challenged (Dormann et al., 2012; Thuiller et al., 2013; Zurell et al., 2009). In fact, species distributions, obtained by summing-up the areas that have been identified as suitable, represents an optimistic "best-case" scenario, wherein species are not limited by their dispersal capacities, so that all suitable areas are immediately fully colonized (Monsimet et al., 2020). At the other extreme, "worst case" scenarios involve that species do not have the dispersal capacities to successfully colonize newly suitable areas (Fig. 3) (Loarie et al., 2008; Thuiller et al., 2005). The major differences that result from the application of 'best-case' and 'worst case' scenarios lead to high levels of uncertainty

(Thuiller et al., 2008). Different methods have been developed to address these issues, including SDM hybrids or dynamic range models (Adams et al., 2015; Alexander et al., 2018; Briscoe et al., 2019; Dullinger et al., 2012; Evans et al., 2016; Fordham et al., 2016; García-Callejas et al., 2016; Lasky et al., 2020; Zurell et al., 2016). SDM hybrids rely on SDMs to predict habitat suitability and then, infer demographic rates. Dynamic range models derive demographic rates directly from the data and model niche preferences as a consequence of demographic processes (see other possible models in Briscoe et al., 2019).

MigClim (Engler et al., 2012) appears as the simplest SDM hybrid, using mechanistic models based on dispersal probabilities constrained by niche preferences (Engler and Guisan, 2009; Zurell et al., 2016). In MigClim, local demographic mechanisms such as mortality and birth, which are important for predicting species range dynamics, are not taken into account (Clark and Gelfand, 2006; Engler et al., 2012; Zurell et al., 2016). Therefore, more complex SDM hybrids, using population models, such as DemoNiche (Nenzén et al., 2012) or Cats (Dullinger et al., 2012), where simple demographic information is needed, and LoLiPop, where abundance data is required (Cabral and Schurr, 2010), have been proposed. However, the use of SDM hybrids is debated as they potentially create circularity problems (Gallien et al., 2010) and because of a poor understanding of how niche preferences derived from SDMs interacts with species demography (Thuiller et al., 2014). This is why dynamic range models (DRM) have been developed to avoid these issues (Zurell et al., 2016). These techniques link demographic rates to environmental factors and derive population dynamic estimates from species abundance and distribution data (Pagel and Schurr, 2012; Zurell et al., 2016). Although all of the presented range dynamic models were shown to perform better than SDMs, there is to date no clear guidelines regarding model choice upon model performance, leading Zurell et al. (2016) to suggest that the chosen model mainly depends on data availability and computational time.

Estimating dispersal in natural populations has, however, long been a challenging issue (Koenig et al., 1996), especially for wind-dispersed organisms due to the spatial and temporal variations in wind conditions and the complexity of environmental features affecting dispersal (García and Borda-de-Água, 2017; Jordano, 2017). While a number of demographic models accounting for local population dynamics have been developed (Zurell et al., 2016), only a few integrate changes in environmental conditions in a spatially explicit context (Lurgi et al., 2015), a key feature to account for local environmental variation.

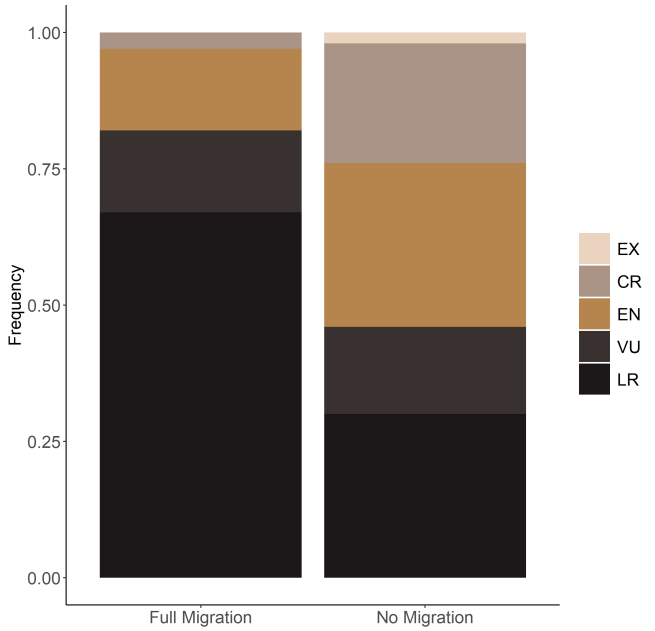

Fig. 3: Proportion of extinct (EX), critically endangered (CR), endangered (EN), vulnerable (VU) and, lower risk (LR) angiosperm species in Europe predicted by projecting species niches onto 2050 climate layers (scenario A1.HadCM3), assuming that newly suitable niches in 2050 are immediately colonized (Full migration scenario) or, to the reverse, never colonized (no migration scenario) (redrawn from Thuiller et al., 2005).

1.4. Bryophytes, a key biological model under climate change

For this thesis, I focused on bryophytes, whose ecopysiological characteristics make them excellent candidates to study the impact of climate change (He et al., 2016; Patiño et al., 2016). This taxon, characterized by a haplo-diplophasic life cycle with a dominant gametophytic phase, is the second most diversified group of land plants, with approximately 20,000 species (Patiño and Vanderpoorten, 2018). Bryophytes can be divided into three groups: Bryophytes in the strictest sense, i.e., mosses, liverworts (Marchantiophyta) and hornworts (Anthocerophyta) (Renzaglia et al., 2007). They are poikilohydric, which means that they are at equilibrium with ambient humidity (Fig. 4). Bryophytes are thus physiologically active when they are humid and enter dormancy upon drying (Vanderpoorten and Goffinet, 2010). Furthermore, bryophytes have no roots and therefore, only rely on atmospheric precipitations for water and nutrients uptakes. Finally, while bryophytes typically exhibit a large cold-tolerance, they are globally sensitive to warm temperatures, displaying significantly lower temperature optima than angiosperms (He et al., 2016; Perera-Castro et al., 2020).

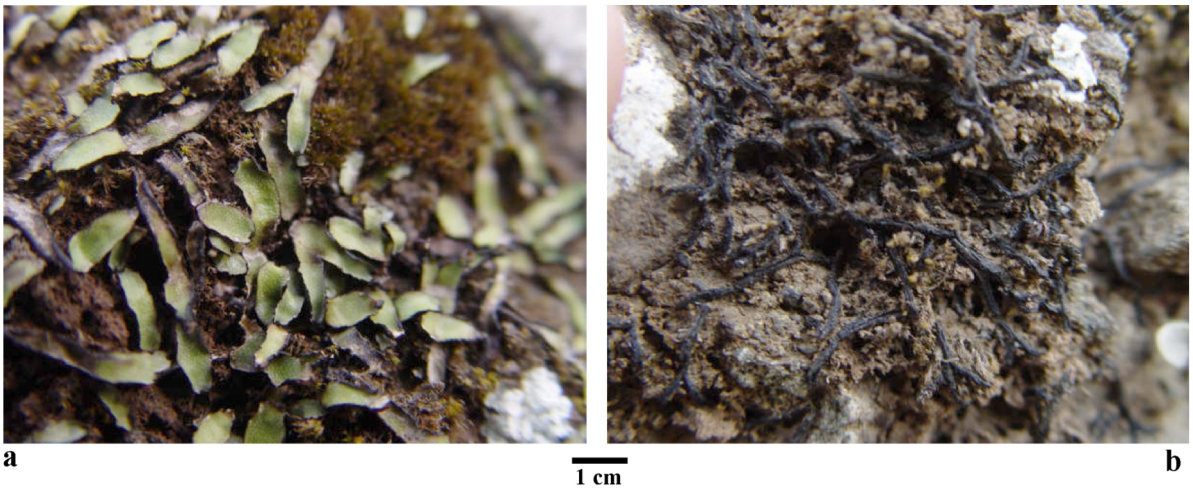

Fig. 4: The thalloid liverwort *Targiona hypophylla*: wet (a) and dry (b) habits (Pictures from Alain Vanderpoorten).

Bryophytes disperse by small spores with a diameter that typically ranges between 10 and 30 µm, and asexual propagules (Patiño and Vanderpoorten, 2018; Vanderpoorten et al., 2019). They primarily disperse by wind (Barbé et al., 2016), although evidence for the role of animal-mediated dispersal, including epizoochory (Chmielewski and Eppley, 2019; Koponen, 1990; Pauliuk et al., 2011) and endozoochory (Boch et al., 2015; Parsons et al., 2007; Russo et al., 2020; Wilkinson et al., 2017), has been increasingly acknowledged. It has therefore been widely accepted that bryophytes exhibit high dispersal capacities (Lönnell et al., 2012) and in fact, similar values of turnover were actually observed among island bryophyte communities and those expected under a null model, according to which species can randomly disperse among islands (Liu et al., 2020). However, these patterns do not necessarily point to the absence of any dispersal limitations in the spore-producing flora. Indeed, analyses of the spatial genetic structure in bryophytes consistently revealed significant isolation-by-distance slopes (Ledent et al., 2020; Vanderpoorten et al., 2019) and, contra Liu et al. (2020), we found in the context of the present thesis that island bryophyte floras exhibit a similar turnover than angiosperm floras along gradients of geographic distance (see Appendix paper S1).

Bryophyte species typically present reduced morphologies and are therefore very sensitive to phylogenetic testing (Vanderpoorten and Shaw, 2010). With the development of molecular phyogenetics, an increasing number of bryophyte species are split into series of species with narrower ranges (Hedenäs, 2017; Hedenäs et al., 2014; Hutsemékers et al., 2012; Medina et al., 2013, 2012; Patiño et al., 2017; Vigalondo et al., 2019). These patterns do not necessarily point to the role of environmental variation as a driver for speciation in the group because, compared to the other land plants, it has long been assumed that bryophytes do not tend to develop ecotypes (see Patiño and Vanderpoorten, 2018 for review). In fact, bryophyte local adaptations can be mitigated due to their excellent dispersal capacities, which allow them to frequently reshuffle their genetic variability even between distant populations (Mikulášková et al., 2015). In addition, mounting evidence congruently points to a significant niche conservatism between sister groups in *Sphagnum* (Johnson et al., 2015; Piatkowski and Shaw, 2019).

Nonetheless, strong genetic structures have increasingly been reported within moss species. Assuming that bryophytes are indeed efficient dispersers, it is tempting to interpret such genetic structuring in terms of local adaptation (Hedenäs, 2018, 2016; Merinero et al., 2020). Evidence for regional ecotypes (Graham et

al., 2019; Greenwood et al., 2019; Vanderpoorten and Durwael, 1999) and for correlation between environmental variation and genetic divergence (Magdy et al., 2016; Mikulášková et al., 2015; Pisa et al., 2013) in fact points to a more important role of local adaptions in mosses than previously thought.

1.5. Objectives

The primary goal of the present thesis was to determine the impact of climate change on bryophytes using an ecological modelling approach. To this aim, we first assessed what is the appropriate taxonomic level to implement niche models and tested the niche conservatism hypothesis in the group. We then developed a newly designed model of dispersal by wind in the context of changing climate and presented an example of application in the case of the European flora.

More precisely, Chapter I addresses the question of the taxonomic level, at which SDMs should be computed. We compare the extent to which model projections generated at the level of species differ from those obtained for intraspecific lineages. Modelling at the level of infraspecific lineages raises a second issue, which is associated with the very small sample sizes that typically characterize molecularly defined lineages, that is: how can ensemble of small models calibrated from very small datasets be evaluated? We propose a solution and in the light of analyses of niche overlap, we finally determine whether models should be calibrated at the level of the species or intraspecific lineages.

In chapter II, we address the question of niche conservatism at different taxonomic scales, and determine its impact on the phylogenetic turnover among communities. More specifically: Is phylogenetic turnover among liverwort floras significant, and if so, to what extent is it explained by macroclimatic variation, pointing to large-scale macroclimatic niche conservatism? How did the correlation between phylogenetic turnover and macroclimatic variation evolve through time?

In chapter III, we develop a hybrid statistical-mechanistic approach that accounts for temporal and spatial variation of both climatic conditions and wind connectivity to predict potential shifts in distribution of wind-dispersed organisms across Europe and present an application in the case of the European bryophyte flora. Our primary questions here are whether such efficient dispersers as bryophytes will indeed successfully track the shift of their suitable area during the next decades, and if dispersal limitations hamper the successful colonization of all newly suitable areas, how many years would be necessary for a full colonization to occur.

2. Chapter I

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RESEARCH PAPER

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Intraspecific differentiation: Implications for niche and distribution modelling

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Abstract

Aim: Mounting evidence suggests that failure of species distribution models to integrate local adaptation hinders our ability to predict distribution ranges, raising the question of whether modelling should be performed at the level of species (clade models) or intraspecific lineages (subclade models), characterized by the restricted availability of occurrence points. While Ensembles of Small Models (ESMs) offer an attractive framework for small datasets, their evaluation remains critical. We address these issues in the case of very small datasets inherent to subclade models and discuss which modelling strategy should be applied based on niche overlap among lineages.

Location: Sweden.

Taxon: Mosses.

Methods: Ensembles of Small Models were evaluated by null models built from randomly sampled presence points. We compared the extent of suitable area predicted by the projections of clade and subclade models. Niche overlap was quantified using Schoener's *D* and Hellinger's*I*metrics, and the significance of these metrics in terms of niche conservatism or divergence was assessed by similarity tests.

Results: We introduced a simple procedure for evaluating ESMs based on the pooling of the statistics used to assess model accuracy from the replicates. Despite fairly high AUC and TSS values, 2 of the 23 subclade models did not perform better than null models and should be discarded. Combined predictions from subclade models contributed, on average, five times more than clade models to the total suitable area predicted by the combination of subclade and clade models. The *D* and *I* metrics averaged 0.45 and 0.71, with evidence for niche conservatism in half of the species and no signal for niche divergence.

Main conclusions: In addition to the assessment of ESM accuracy based on the simple procedure described here, we recommend that ESMs should be systematically evaluated against null models. Lumping or splitting occurrence data at the intraspecific level substantially impacted model projections. Given the poor performance of models based on small datasets, even when employing ESMs, we pragmatically suggest that, in the absence of evidence for niche divergence during diversification of closely related intraspecific lineages, SDMs should be based on all available occurrence data at the species level.

KEYWORDS
Boyce index, bryophytes, local adaptation, niche conservatism, niche similarity, species distribution models, taxonomy

1 | INTRODUCTION

Niche-based species distribution models (SDMs) are powerful tools connecting species occurrence data to environmental variables with a wide range of applications in ecology, climate change biology, conservation biology and systematics (Guisan et al., 2017). These models are also called ecological niche models (ENMs), habitat suitability models (HSMs) and several other names (see Guisan et al., 2013, Supporting Information S1; Araújo et al., 2019, Table S1.1), yet are usually fitted with the same data and techniques (but see McInerny & Etienne, 2013; Peterson and Soberón, 2012). Therefore, following Araújo et al. (2019), we hereafter use the term SDM for convenience.

Like many biodiversity analyses, SDMs have traditionally been conducted at the species level (hereafter clade models, Pearman et al., 2010). Mounting evidence for cryptic speciation, which results in taxa that cannot readily be distinguished morphologically but underwent divergent evolutionary histories (Struck et al., 2018) raises, however, the question of whether modelling should be performed at the level of cryptic species or even intraspecific lineages (hereafter subclade models, Pearman et al., 2010; Smith et al., 2019). The niche conservatism hypothesis predicts low niche differentiation between species over evolutionary time scales (Peterson et al., 1999; Wiens, 2004; Wiens & Graham, 2005). The role of local adaptation in species diversification has, however, been increasingly acknowledged (Chardon et al., 2020; Peterson et al., 2019; Sork, 2017), with major consequences for our ability to accurately infer species niches and, in particular, predict future distributions in the context of climate change (Hällfors et al., 2016; Maguire et al., 2018; Peterson et al., 2019; Valladares et al., 2014; Yannic et al., 2014).

The fact that cryptic species and intraspecific lineages are characterized by molecular data, so that specimens are assigned to a given lineage after genotyping analysis, typically results in a very small number of actual observations as compared to the vast amount of distribution data available from databases such as GBIF at the species level. The comparatively small number of actual observations at the intraspecific level readily raises issues related to sample size for both model calibration and evaluation (Maguire et al., 2018). Ensembles of Small Models (ESMs) have been developed to address the issue of model calibration with small datasets (Breiner et al., 2015, 2018; Lomba et al., 2010). ESMs compute bivariate models and then combine all possible bivariate models into an ensemble . By averaging simple small models to an ensemble, ESMs avoid overfitting without losing explanatory power through reducing the number of predictor variables, and were shown to perform significantly better than standard SDMs with rare species (Breiner et al., 2015). The evaluation of model performance based on small datasets remains, however, critical (Jiménez-Valverde, 2020). For ESMs, Breiner et al. (2015, 2018) recommended to compute accuracy values such as AUC and TSS by keeping a proportion of the data for model calibration and using the remaining of the data for evaluation, replicating this operation n times and then average the values of the statistics across replicates. For a dataset with 10 presences and keeping 20% of hold-out data for calibration, this would leave as few as 2 points per replicate for model evaluation, whereas Jiménez-Valverde (2020) most recently recommended that minimum sample sizes of 20 (10 presences and 10 true absences) should be used when attempting at evaluating models through bootstrapping. Furthermore, the implementation of widely used model accuracy statistics, such as AUC, when applied to presence-only data, has been questioned. In fact, the number of pseudo-absences is largely higher than that of presences, and including more absences that are environmentally more distant from the species' presences increases the fraction of correctly predicted absences (specificity), results in unduly high AUC values (Jiménez-Valverde, 2012; Lobo et al., 2008). Van Proosdij et al. (2016) therefore introduced a validation procedure based on the comparison of the performance of models calibrated from actual data with that of null models calibrated from pseudo-absences.

Here, we address these issues through analyses of niche modelling, taking advantage of recently published data on intraspecific differentiation in Swedish mosses (Hedenäs, 2019). Mosses exhibit reduced morphologies and species circumscriptions based on morphology are, therefore, vulnerable to phylogenetic testing (Vanderpoorten & Shaw, 2010). With the advance of molecular phylogenetics, there has been a clear tendency for the split of broadly circumscribed species with trans-oceanic distribution ranges into series of species with much narrower ranges (Hutsemékers et al., 2012; Medina et al., 2012, 2013; Hedenäs et al., 2014; Hedenäs, 2017; Patiño et al., 2017; Vigalondo et al., 2019). Mounting evidence for strong geographic structure within phylogenetically redefined species (Hedenäs, 2016, 2018) further raises concerns about potential ecotypic differentiation, challenging the application of SDMs. Previous experimental work suggests that, in contrast with the vast majority of seed plants, bryophytes do not tend to develop ecotypes, but rather display an inherent broad ability to cope with environmental variation (see Patiño and Vanderpoorten, 2018 for a review). Furthermore, bryophytes are highly dispersive, enabling them to effectively migrate across long distance, so that even distant populations may regularly reshuffle their genetic variability, possibly neutralizing local adaptations (Mikulášková et al., 2015). Nevertheless, reports of regional differences in niche characteristics (Graham et al., 2019; Shaw, 1985; Vanderpoorten & Durwael, 1999), and mounting evidence for correlated patterns of genetic divergence and environmental variation (Hutsemékers et al., 2010; Magdy

et al., 2016; Mikulášková et al., 2015; Pisa et al., 2013; Szövényi et al., 2009), suggest that adaptation may play a more important role in bryophytes than previously thought.

In this context, we address the following questions: (1) how can ESMs calibrated from very small datasets be evaluated? (2) To what extent do model projections generated at the level of species or genetically differentiated intraspecific lineages differ? (3) In the light of analyses of niche overlap, should models be calibrated at the level of the species or intraspecific lineages?

2 | MATERIALS AND METHODS

2.1 | Study area and data collection

Hedenäs (2019) investigated intraspecific differentiation in 10 moss species across Sweden based upon variation at 1–2 nDNA and 1–4 cpDNA loci. Phylogeographic analysis resolved 2–4 well-supported clades of 4–93 specimens within eight species. These clades represent genetic lineages that are currently considered as cryptic taxa but not formally recognized taxonomically. In *Sarmentypnum exannulatum*, incongruence between ITS and cpDNA loci led to the identification of different nDNA and cpDNA lineages, which were kept separate in the present analyses. Only lineages including more than 10 specimens were kept. To characterize the climatic conditions under which each lineage is currently distributed, data for 19 bioclimatic variables at a 1 km resolution were downloaded from WorldClim 1.4 (Hijmans et al., 2005). In order to avoid multicollinearity, we computed a Pearson correlation coefficient matrix among climatic variables from 10,000 background points randomly sampled in the study area with the sp package (Bivand et al., 2013; Pebesma & Bivand, 2005). Applying the rule of thumb that correlation coefficients of predictors should not exceed $r = 0.7$ (Breiner et al., 2015; Dormann et al., 2013), we selected six variables, namely, bio 1 (annual mean temperature), bio3 (isothermality), bio 7 (temperature annual range), bio 8 (mean temperature of the wettest quarter), bio 12 (annual precipitation), bio 15 (precipitation seasonality) and bio 16 (precipitation of wettest quarter).

To overcome the issue of spatial autocorrelation, spatial disaggregation of the data, either spatially or environmentally, has been discussed, but yielded conflicting results in terms of model fit (contrast, e.g. Anderson and Raza, 2010 vs. Varela et al., 2014 for geographic filtering and Varela et al., 2014 vs. Castellanos et al., 2019 for environmental filtering). To assess the level of spatial autocorrelation in the data, we computed the number of individuals located at <1 km from each other. For environmental autocorrelation, we applied a grid onto the space defined by the first two components of a principal component analysis (PCA), as recommended by Castellanos et al. (2019). The PCA was performed on the correlation matrix among the seven selected climatic variables at each occurrence point in R 3.5.3 (R Core Team, 2019) with the 'synoptReg' package (Lemus-Canovas et al., 2019). The first two axes accounted for 77% of the variance. The grid divided the range of each component into equal interval bins of size 100. Applying these two filters to the data would lead to an average loss of only 5% and 8% of the data, respectively, suggesting very limited autocorrelation, so that all the data were kept in the analyses.

2.2 | Species distribution models

Niche-based species distribution modelling was performed with ESMs. Although ensemble predictions based on combined modelling techniques were shown to perform better compared to single modelling techniques (Marmion et al., 2009), Breiner et al. (2015) found that averaging ESMs across modelling techniques does not further increase mosdel performance. Breiner et al. (2015) therefore concluded that there is thus no need to build ESMs based on several modelling techniques, which are more complex and more computationally intensive than ESMs based on a single modelling technique. Based on Breiner et al. (2018), who further recommended that, when the overall aim is to produce models with a high predictive performance, the best choices are ESMs with artificial neural networks and gradient boosting machines (GBM; Friedman, 2001), we employed the latter in the present study with the default parameters in biomod2 (Thuiller et al., 2019), that is, a Bernouilli distribution, 2,500 trees to fit, a tree complexity of 7, a minimum of 5 observations in the terminal nodes of the trees, a bag fraction of 0.5 and 3 cross-validation.

The procedure followed to calibrate and evaluate the performance of the ESMs is illustrated in Appendix S2 and was implemented with the ecospat package (Broennimann et al., 2017; Di Cola et al., 2017). For each clade and subclade model, 10 replicates of 21 bivariate models and their ensemble were run, using 80% of the occurrence data to train them and the remaining 20% (hold-out data) to evaluate them. We employed the species occurrence data and 10,000 pseudo-absences randomly selected from the entire area with the sp package. We used the same set of pseudo-absences among conspecific lineages but different sets among species. Following Breiner et al. (2015), pseudo-absences and occurrence data were weighted equally in the models.

We built an ensemble model prediction for each replicate by calculating a weighted average of the outputs of the 21 bivariate models, weighting each bivariate model by its Somers' *D* (i.e. rescaled area under the ROC curve, AUC) values to improve reliability of the model predictions (Araújo and New, 2007). Bivariate models with a Somer's $D \leq 0$ (i.e. AUC≤0.5 and, hence, equal or worse than a random model) were set to zero and, thus, were not included in the ensemble model.

Model performance was assessed through Boyce index, which is designed for presence-only data (Hirzel et al., 2006), as well as the AUC and the maximum true-skill statistic (maxTSS), which were primarily designed for presence-absence data (Phillips et al., 2009) and were, hence, computed from the occurrence and pseudo-absence points. Although widely used for the evaluation of models based on presence-only data (Bradter et al., 2018; Lobo & Tognelli, 2011),

AUC has, however, been criticized in such conditions because including more absences that are environmentally more distant from the species' presences unduly increases the specificity, resulting in higher AUC values (Jiménez-Valverde, 2012; Lobo et al., 2008).

Breiner et al. (2015, 2018) recommended to compute AUC, maxTSS and Boyce index from the hold-out data for each replicate, and then to average the obtained values (per metric) across replicates. Such a procedure would leave as few as 2 points per replicate for model evaluation in the present study. Because minimum sample sizes of 20 (10 presences and 10 true absences) are recommended when attempting at evaluating models through bootstrapping (Jiménez-Valverde, 2020), we decided to use a new approach pooling the suitability values of the hold-out data across replicates. As the same presence point is likely to be sampled in multiple replicates, the suitability values for each presence point were averaged across replicates. This generated a series of suitability values independent from the data used to calibrate the models, with a size roughly equal (as some occurrence points may not have been sampled in any of the 10 replicates) to that of the number of occurrence data. These suitability values were then combined with the pseudo-absence points and used to compute the AUC, maxTSS and Boyce index of the ESM for each clade and subclade models with the 'ecospat' (Broennimann et al., 2017; Di Cola et al., 2017) and 'dismo' (Hijmans et al., 2017) packages.

We further assessed whether our models performed better than random predictions using the method proposed by van Proosdij et al. (2016). We generated null models by randomly selecting the same number of pseudo-absence points as occurrence data 100 times. These 100 sets of pseudo-absence points were treated as presences and null ESMs were generated by weighting the bivariate models according to their AUC. These null models were then evaluated through their AUC, maxTSS and Boyce index with the procedure described above, and the ESMs based on actual occurrence data were considered significant if less than 95% of the null models exhibited higher AUC, maxTSS and Boyce index.

To generate the final ESM for each clade and subclade, each of the 21 bivariate models was recomputed from all the occurrence data (as recommended by James et al., 2013; see Guisan et al., 2017). Any bivariate model with an average Somers'*D* ≤0 across the 10 replicates was not included in the final ESM. The contribution of the remaining bivariate models was weighted by their average Somer's *D* across the 10 replicates to produce the final ESM, which was projected onto present, future (Max-Planck-Institut für Meteorologie [MPI] under three representative concentration pathways [RCP]: 2.6, 4.5 & 8.5) and mid-Holocene (about 6,000 years ago) climatic layers. We reported the entire procedure following the ODMAP (Overview, Data, Model, Assessment and Prediction) protocol (Zurell et al., 2020) in Appendix S3.

To assess the difference between clade and subclade models on predicted ranges, we subsequently binarized the models. The values of the continuous suitability index were binarized, for each clade and subclade model, by maximizing the sum of sensitivity and specificity (maxSSS), as recommended by Liu et al. (2013, 2016) for presence-only data, with the 'raster' package (Hijmans, 2019). We further performed a sensitivity analysis by increasing and decreasing the value of the threshold from +0.05 to +0.20 and −0.05 to −0.15 around the optimal threshold value. We finally summed up the pixels that were identified as suitable when projecting, for each species, the binarized clade and subclade models to quantify the differences in the extent of suitable areas inferred from these models.

2.3 | Niche overlap and divergence metrics

Niche overlap among lineages was measured via Schoener's *D* and a modified Hellinger's *I* metric (Warren et al., 2008). The *D* and *I* metrics were computed from climatic variation under present conditions summarized by the first two PCA components via the 'ecospat' package (Broennimann et al., 2017; Di Cola et al., 2017). We first used as presence points all the pixels identified as suitable by the projections of the SDMs for each intraspecific lineage onto the studied geographic background. To address the issue that niche conservatism or expansion should be tested only within environmental conditions that are accessible to both lineages being compared to avoid spurious effects of model extrapolation (Guisan et al., 2014; Qiao, Escobar et al., 2017), we performed a multivariate environmental similarity surface (MESS) analysis (Elith et al., 2010) as implemented by the 'modEvA' package (Barbosa et al., 2016). The MESS analysis measures the similarity of any given pixel in the range of a lineage A to a reference set of pixels in the range of another lineage B with respect to the chosen predictor variables. A pixel with a positive value in the A range indicates that it falls within the range of environmental values present in the B range, while a pixel with a negative value indicates that at least one variable has a value that is outside of the range of environmental values present in the B range. MESS values of 0 or above were therefore used to define areas of analogous climates among lineages, and negative values as non-analogous climates. Based on the MESS analysis, we filtered out all the pixels that were climatically suitable to A (as inferred by SDMs), but were characterized by climate conditions never experienced by B (non-analogous climates) and vice versa. The implementation of the MESS analysis leads to a decrease in statistical power owing to reduced sample sizes but is, as Qiao, Escobar, et al. (2017) emphasized, far less prone to spurious conclusions of niche shift that are made when the two entities being compared are observable only against distinct environmental backgrounds. Because Broennimann et al. (2012) demonstrated that such SDM-based approaches tend to return high levels of niche overlap, we also measured niche overlap directly from the present climatic conditions that prevail at the level of actual occurrence records with the 'ecospat' package (Broennimann et al., 2017; Di Cola et al., 2017).

Warren et al. (2008) introduced two tests aiming at determining whether two niche models are identical (equivalency test) or more similar (pointing to niche conservatism) or different (pointing to niche divergence) than would be expected by chance (similarity test). Although both tests are still commonly employed (e.g. Hamid et al.,

2019; Louppe et al., 2019), the equivalency test is prone to unduly rejecting the null hypothesis of niche identity (Peterson, 2011). As previously shown by simulations (Broennimann et al., 2012), its null hypothesis was indeed also systematically rejected for all of the lineages investigated here, and we therefore focused on the similarity test. As presented in Broennimann et al. (2012), the similarity test compares the actual similarity (niche overlap) of the environmental niches of A and B, as assessed by *I* or *D* values, to the distribution of similarities obtained by comparing the environmental niche of A to an environmental niche obtained by randomly shifting the entire observed density of occurrences of B among the available environment in the study area. The same procedure is repeated for species B. This analysis is repeated 100 times in each direction (A to B, or B to A) to construct the distribution of simulated *I* or *D* values. If the observed *I* and *D* values fall within the density of 95% of the simulated values, the null hypothesis cannot be rejected. The null hypothesis is rejected if the actual niche similarity between A and B falls outside of the 95% confidence limits of the null distribution. We tested the hypothesis that the observed *I* and *D* values are higher (the niches of the two lineages are more similar than would be expected by chance) or lower (the niches of the two lineages are less similar than expected by chance) than the simulated values, pointing to niche conservatism and niche divergence, respectively, with the procedure implemented in the 'ecospat' package (Broennimann et al., 2017; Di Cola et al., 2017). The niche similarity test was performed using both climatically suitable pixels restrained with the MESS analyses and actual occurrence data.

3 | RESULTS

Clade and subclade models exhibited average AUC, maxTSS and Boyce index of 0.81 ± 0.05, 0.51 ± 0.07 and 0.93 ± 0.04 and of 0.84 ± 0.10, 0.60 ± 0.20 and 0.86 ± 0.07 respectively (Table 1). These models were significantly better than null models in 30 of the 32 models evaluated based on AUC and maxTSS, but in only 25 of the 32 models based on the Boyce index (Table 1).

The impact of the taxonomic level at which SDM are computed on the extent of predicted suitable area when models are projected onto present, future (scenarios MPI 2.6, 4.5 and 8.5) and past (mid-Holocene) climatic layers is summarized in Table 2, Figure 1 and Appendix S5. Subclade models contributed, on average, about five times more than clade models to the total suitable area predicted by the combination of subclade and clade models. At time present, for example, 40.6% ± 22.2% of that total suitable area was on average predicted by subclade models only against 8.6% ± 6.4% for clade models. The results were robust to variations in the binarization threshold value of −0.05 to −0.15 and +0.05 to +0.20 around the optimal value, although an increase in the proportion of clade versus subclade models to identify suitable pixels with increasing threshold values was observed (Appendix S5). Similar, but even higher trends were observed for the projection of the models under past and future climatic layers, with, for example, 51.9% ± 28.6% of that total suitable area being, on average, predicted by combined subclade models only against 8.2% ± 6.2% for clade models, under scenario of climate change MPI4.5.

Niche overlap under present climate conditions between conspecific lineages ranged between 0.19 and 0.79 with an average of

TABLE 1 AUC, MaxTSS and Boyce index of the ensemble of small models used to model the niche of eight moss species at the level of their entire range in Sweden (clade models) and for each intraspecific lineage (subclade models A, B, C, D) obtained after pooling the suitability values of the hold-out data (20% of the data) of each of the 10 replicates. The suitability values obtained for each individual occurrence point were averaged across replicates. Values in bold were higher than those observed in >95% of 100 null models calibrated from randomly sampled points instead of actual observations

		Test sets		
Species		AUC	MaxTSS	Boyce
Drepanocladus trifarius	Clade	**0.83**	**0.54**	**0.96**
	A	**0.79**	**0.51**	**0.94**
	B	**0.87**	**0.57**	**0.83**
Meesia uliginosa	Clade	**0.85**	**0.59**	**0.91**
	A	**0.78**	**0.49**	**0.76**
	B	**0.93**	**0.78**	0.88
Myurella julacea	Clade	**0.85**	**0.55**	**0.97**
	A	**0.83**	**0.58**	**0.89**
	B	**1.00**	**0.98**	0.74
Oncophorus virens	Clade	**0.88**	**0.68**	**0.87**
	A	**0.80**	**0.46**	**0.87**
	B	**0.98**	**0.87**	**0.81**
Racomitrium lanuginosum	Clade	**0.72**	**0.46**	**0.88**
	A	0.62	0.23	**0.86**
	B	0.62	0.31	**0.89**
	C	**0.95**	**0.88**	0.68
Sarmentypnum exannulatum CHL	Clade	**0.77**	**0.48**	**0.92**
	A	**0.76**	**0.44**	**0.95**
	B	**0.94**	**0.78**	0.87
	C	**0.85**	**0.56**	**0.98**
Sarmentypnum exannulatum ITS	Clade	**0.79**	**0.46**	**0.97**
	A	**0.84**	**0.56**	**0.97**
	B	**0.79**	**0.51**	**0.89**
	C	**0.86**	**0.56**	**0.87**
	D	**0.81**	**0.61**	0.80
Scorpidium cossonii	Clade	**0.82**	**0.49**	**0.97**
	A	**0.81**	**0.47**	**0.98**
	B	**0.93**	**0.80**	**0.85**
Tortella tortuosa	Clade	**0.75**	**0.39**	**0.94**
	A	**0.68**	**0.28**	**0.86**
	B	**0.96**	**0.85**	0.81
	C	**0.91**	**0.66**	0.87

TABLE 2 Differences in the extent of suitable area under present, future (scenarios MPI2.6, 4.5 and 8.5) and past (mid-Holocene) conditions, obtained by projections of binarized niche models in eight moss species in Sweden, between models computed at the level of cryptic intraspecific molecular lineages (subclade models, each inferred from the presence points for each of the n lineages recognized within a species) and broadly defined morphological species concept (clade models, one per species, inferred from all the presence points available for that species regardless of intraspecific genetic differentiation). For each species, all the pixels identified as suitable by (i) the clade model, but not by the subclade models (Nc, blue colour in Figure 1); (ii) the subclade models, but not the clade model (Nsc, equal to the summation of suitable pixels identified by each of the n subclade models, red colour in Figure 1) and (iii) jointly identified by clade and subclade models (Nj, green colour in Figure 1) are summed-up to define the maximum number of suitable pixels for a species, N. The contribution of clade and subclade models to N is then computed as follows: A: Nsc/N*100; B: Nc/N*100; C: Nj/N*100. n represents the number of subclades defined within each species. *Sarmentypnum exannulatum* CHL and ITS represent separate lineages defined by incongruent cpDNA and nDNA loci

		Present			MPI2.6			MPI4.5			MPI8.5			Mid-Holocene		
Species	***n***	**A**	**B**	**C**	**A**	**B**	**C**	**A**	**B**	**C**	**A**	**B**	**C**	**A**	**B**	**C**
Drepanocladus trifarius	2	8.0	14.4	77.5	13.7	16.4	69.8	10.0	17.5	72.4	12.0	16.9	71.1	10.0	18.2	71.9
Meesia uliginosa	2	34.0	8.8	57.2	35.9	9.1	54.9	32.2	8.0	59.8	41.1	8.8	50.1	39.6	7.1	53.3
Myurella julacea	2	25.9	4.2	69.9	25.7	8.0	66.3	29.0	4.3	66.7	28.1	5.9	66.0	24.6	5.3	70.1
Oncophorus virens	2	16.8	11.9	71.4	26.8	7.8	65.4	21.8	10.5	67.7	25.3	9.4	65.3	13.5	18.4	68.1
Racomitrium lanuginosum	3	54.8	19.9	25.3	62.3	12.4	25.3	67.1	14.7	18.2	67.7	12.5	19.8	66.9	15.7	17.4
Sarmentypnum exannulatum CHL	3	60.4	3.1	36.5	80.4	1.1	18.5	81.3	1.5	17.2	83.6	0.8	15.5	56.7	1.8	41.5
Sarmentypnum exannulatum ITS	4	56.1	2.4	41.4	76.5	4.2	19.2	78.0	4.2	17.8	80.2	4.4	15.4	58.1	1.6	40.3
Scorpidium cossonii	2	62.4	0.8	36.8	82.0	0.0	17.9	84.9	0.0	15.1	81.4	0.0	18.6	83.9	0.3	15.9
Tortella tortuosa	3	62.7	12.0	25.3	62.3	11.8	25.9	62.8	13.2	24.0	69.0	10.6	20.7	58.3	20.8	20.8
Mean (±*SD*)		40.6 ± 22.2	8.6 ± 6.5	49.0 ± 20.3	51.8 ± 26.4	7.9 ± 5.4	40.4 ± 23.0	51.9 ± 28.6	8.2 ± 6.2	39.9 ± 25.7	54.3 ± 27.7	7.7 ± 5.5	38.0 ± 24.5	45.7 ± 25.3	9.9 ± 8.3	44.4 ± 22.9

0.43 for Schoener's *D* and between 0.30 and 0.97 with an average of 0.71 for Hellinger's *I* metrics, respectively, when using pixels identified as climatically suitable as occurrence records (Figure 2). The null hypothesis of the similarity test could not be rejected in four of the eight investigated species. For *Oncophorus virens*, both cpDNA and ITS lineages defined within *Sarmentypnum exannulatum*, *Scorpidium cossonii* and *Tortella tortuosa*, both observed *D* and *I* metrics were significantly higher than expected under the null hypothesis, indicating niche conservatism (Figure 2). The same results were obtained when using actual occurrence records, but with a slightly lower confidence of rejecting the null hypothesis (Appendix S4).

4 | DISCUSSION

Small sample sizes affect model calibration, but also evaluation, and minimum sample sizes of 20 (10 presences and 10 true absences) are recommended when attempting at evaluating models through bootstrapping (Jiménez-Valverde, 2020). Computing AUC, maxTSS and Boyce index from the hold-out data for each replicate and averaging them across replicates, as recommended by Breiner et al. (2015, 2018), leads to very small sample sizes for test sets. This is why we suggest here to evaluate ESMs by pooling the suitability values of the hold-out data across replicates. As the same presence point is likely to be sampled in multiple replicates, the suitability values for each presence point can be averaged across replicates to avoid pseudo-replication, generating a series of suitability values independent from the data used to calibrate the models. These suitability values can then be combined with the pseudo-absence points to assess model performance. As a result, model performance is computed from roughly the total number of occurrence data available instead of averaging AUC, maxTSS and Boyce index computed from very small subsets of hold-out data. Despite relatively high values of AUC, TSS and Boyce index, 2 of the 32 ESMs did, however, not exhibit significantly higher AUC and maxTSS values than those that would be expected to be obtained by chance from null models, as proposed by van Proosdij et al. (2016). This evaluation procedure based on the construction of null models calibrated from pseudo-absences thus appears as a useful tool to discard unreliable models based on very small sample sizes, and we therefore recommend its implementation for ESM evaluation in general.

Distinguishing intraspecific differentiation when modelling species distributions had substantial consequences, as the combined projection of subclade models onto past, present and future climatic layers consistently predicted larger ranges than those resulting from clade models (Figure 1, Table 2). Our results thus support the idea that lumping and splitting produce very different niche and distribution estimates (Hällfors et al., 2016). In contrast with the present results, Maguire et al. (2018), Moto-Vargas and Rojas-Soto (2016) and Cacciapaglia and Woesik (2018) reported that clade models tend to predict larger areas of suitable conditions than combined subclade models. Maguire et al. (2018) suggested that clade models may smooth across the climate–distribution relationships that are identified by subclade models, capturing a broader niche representing more potential combinations of climate conditions. Alternatively, we suggest that this result may also arise from overfitting at the level of the subclade models, which are based on lower number of occurrence data than clade models. In turn, and in line with the present results, Pearman et al. (2010), Oney et al. (2013) and Valladares et al. (2014) reported that combined subclade models tend to predict larger areas of suitable conditions than clade models because subclade models can predict suitable areas that are geographically peripheral to areas predicted suitable by clade models (Pearman et al., 2010). We found that this result was robust to departures of the binarization threshold from the optimal value identified by maxSSS, except in one species (*O. virens*) (Appendix S6).

The substantial differences between the projections of clade and subclade models raise the question of the level at which modelling should be performed. To address this question, two criteria have been proposed based on model accuracy and analyses of niche overlap (Smith et al., 2019). AUC and MaxTSS are dependent on prevalence, and hence, not comparable among models based on different sampling sizes (Somedi et al., 2017). As Smith et al. (2019) emphasized, it is therefore challenging to compare clade and subclade models on an equal basis because of factors that are difficult to control, including range size and geographic extent, sample size and autocorrelation between training and test sets that varies in strength depending on whether occurrences are combined or divided.

The second criterion that could be employed to help deciding whether clade or subclade models should be applied is based on niche overlap analyses and niche similarity tests (Broennimann et al., 2012; Warren et al., 2008), which failed here to demonstrate niche divergence. Instead, evidence for niche conservatism was found in half of the species considered, in line with broad support for this mechanism (Peterson et al., 1999) and emerging evidence for it in bryophytes (Johnson et al., 2015; Piatkowski & Shaw, 2019). In bryophytes, evidence for niche expansion outside of the native range in invasive species is lacking (Mateo et al., 2015), but correlations between genetic and ecological distances, potentially pointing to ecological specialization, have been recurrently reported (Hutsemékers et al., 2010; Magdy et al., 2016; Mikulášková et al., 2015; Pisa et al., 2013; Szövényi et al., 2009). Whether such correlations truly point to local adaptation remains, however, to be demonstrated. In fact, two molecular lineages identified within the peatmoss *Sphagnum magellanicum* and exhibiting allopatric ranges were shown to respond equally to climate treatments in common garden experiments (Schwarzer & Joshi, 2017). In line with Schwarzer and Joshi (2017), we suggest that the allopatric ranges exhibited by intraspecific moss lineages may originate from historical factors, such as local extinctions and dispersal, and competition between the herb and bryophyte layers (Mod, Heikkinen, le Roux, Vare, et al., 2016) and within the bryophyte community (Udd et al., 2016) rather than local adaptation. In the absence of evidence for niche divergence, and given the problems of model calibration and evaluation from small datasets, even when applying specifically designed techniques such as ESMs, we therefore support the idea that clade models should be applied (Hällfors et al., 2016). Using simulated data allowing an assessment of competing model performance, Qiao, Peterson, et al. (2017) in

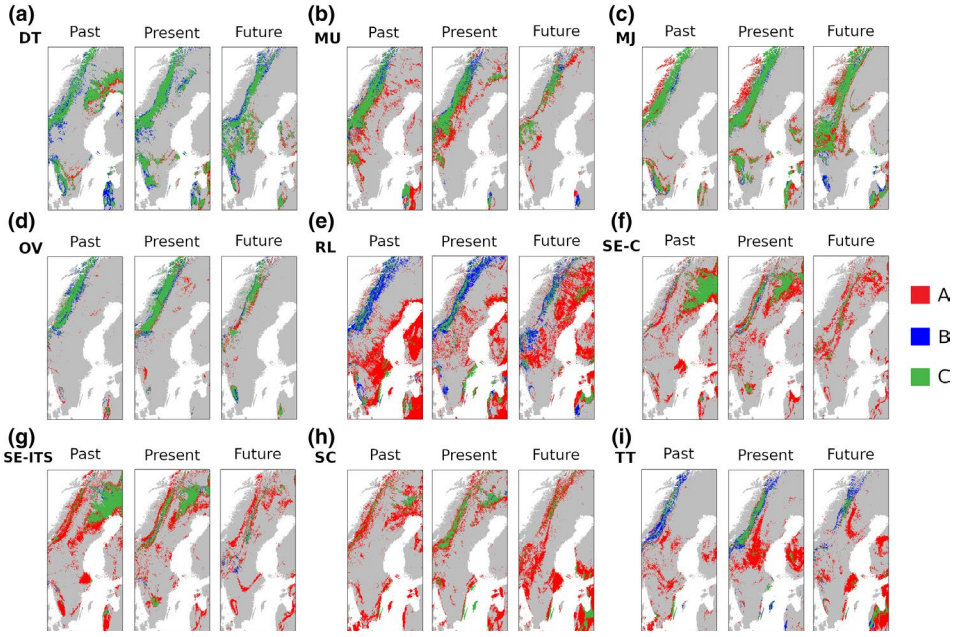

FIGURE 1 Differences in the extent of suitable area under past (mid-Holocene), present and future (scenario MPI 8.5, see Appendix S5 for scenarios MPI2.6 and 4.5) conditions for eight moss species in Sweden between models computed at the level of cryptic intraspecific molecular lineages (subclade models) versus broadly defined morphological species concept (clade model). Areas identified as suitable by the projections of subclade models, but not by clade models, are shown in red (A). Areas identified as suitable by clade models, but not by subclade models, are shown in blue (B). Areas identified as suitable by both clade and subclade models are represented in green (C). DT: Drepanocladus trifarius; MU: Meesia uliginosa; MJ: Myurella julacea; OV: Oncophorus virens; RL: Racomitrium lanuginosum; SE-C: Sarmentypnum exannulatum CHL; SE-ITS: Sarmentypnum exannulatum ITS; SC: Scorpidium cossonii; TT: Tortella tortuosa. Sarmentypnum exannulatum CHL and ITS represent separate lineages defined by incongruent cpDNA and nDNA loci [Colour figure can be viewed at wileyonlinelibrary.com]

fact showed that, in the case of groups of rare, sister species, the projection of models built at the level of the pooled distributions of sister species (clade models) better match the known distribution of individual species (subclade models) when sister species share similar niches.

Smith et al. (2019) argued against the use of niche similarity tests to decide whether fitting models at the levels of clade or subclade because two lineages shown to be more similar than expected by chance may still sufficiently differ in their environmental tolerances, so that their niches would be best modelled by splitting. In fact, the four species for which a signature of conservatism was found were not systematically the ones for which the mismatch between clade and subclade models was the lowest. While we certainly agree with Smith et al. (2019) that evidence for (or lack of) selectively based niche differentiation should ideally be based upon progeny tests and common garden experiments or association mapping of alleles with observed phenotypic differences across populations, such evidence is almost completely lacking in non-model organisms like mosses, wherein reduced morphologies further hamper the possibility to use aspects of life history or functional traits expected to experience strong selection.

In conclusion, we suggest that niche description and an assessment of niche overlap using the *I* and *D* metrics represent a useful contribution in the context of an increasing interest for integrative taxonomic approaches (Raxworthy et al., 2007), especially in small-sized organisms with reduced morphology such as bryophytes (Vigalondo et al., 2019, and references therein). Given the genetic forces underlying the speciation process, it is, in fact, not appropriate to use morphological diagnosability as the sole criterion for species recognition (Egge & Simons, 2006). In the present study, where lack of significant niche divergence among lineages is coupled with the absence of any morphological divergence between them, lineages may not deserve recognition at the species level, although their genetic distinctiveness and mostly allopatric ranges suggest that they may be recognized as different units for conservation (Hedenäs, 2016, 2017, 2018, 2020).

Marcer et al. (2016) recommended that such intraspecific genetic differentiation should guide the design of SDMs studies. We suggest, however, that, in the absence of solid evidence for niche divergence among molecularly defined lineages, SDMs should be based on all available occurrence records at the level of species, ideally redefined based on molecular data or, in the absence of the latter, based on morphological species concepts. This will help generating datasets of sufficiently large size for modelling in organisms whose distributions are typically poorly documented, as in the case of complexes of rare species (Qiao, Peterson, et al., 2017). The degree of niche conservatism, however, decreases with phylogenetic depth (Peterson, 2011). Although the identity of bryophyte species with extremely large disjunctions has been confirmed in some instances (Vigalondo et al., 2016), taxonomic revisions in the light of molecular evidence recurrently showed that segregate species from a previously large morphological species concept and encompassing large, trans-continental ranges, may be polyphyletic and sometimes remotely related (Damayanti et al., 2012; Hutsemékers et al., 2012;

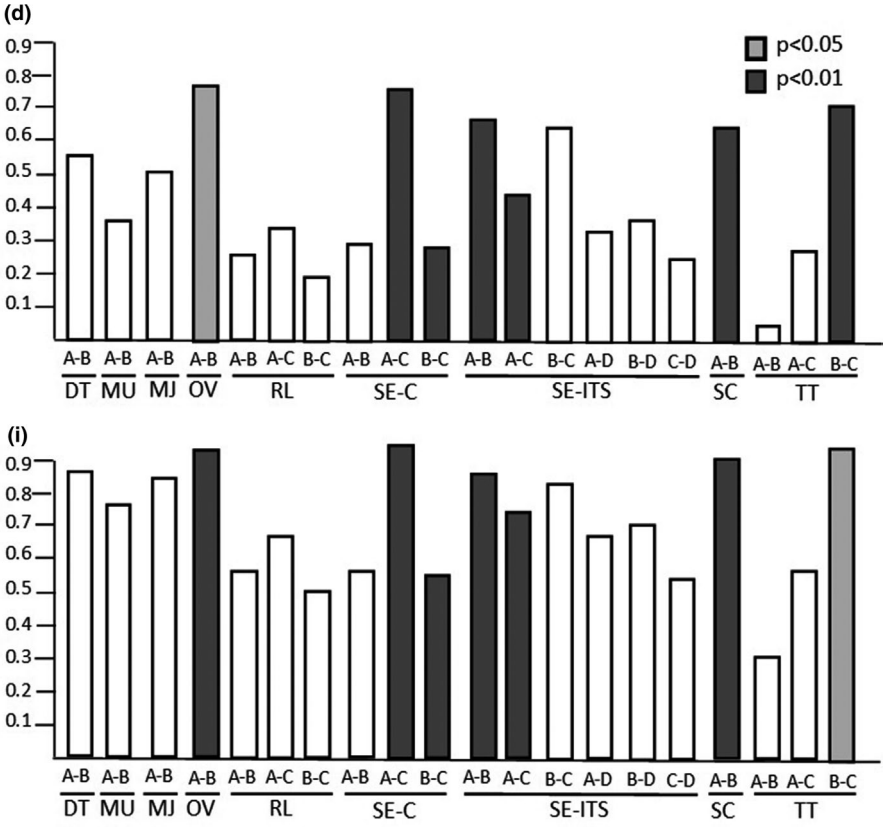

FIGURE 2 Schoener (*D*) and Hellinger (*I*) niche overlap metrics among lineages (A, B, C, D as defined in Appendix S1) identified by phylogeographic analyses in eight moss species in Sweden using climatically suitable pixels under present climate conditions for each lineage as presence points. White, light grey and dark grey bars indicate the significance level (>0.05, <0.05 and <0.01, respectively) among lineages for a unilateral test (niche similarity greater) determining whether the observed values significantly depart from the null hypothesis. DT: *Drepanocladus trifarius;* MU: *Meesia uliginosa*; MJ: *Myurella julacea*; OV: *Oncophorus virens;* RL: *Racomitrium lanuginosum*; SE-C: *Sarmentypnum exannulatum* CHL; SE-ITS: *Sarmentypnum exannulatum* ITS; SC*: Scorpdidium cossonii*; TT: *Tortella* tortuosa. *Sarmentypnum exannulatum* CHL and ITS represent separate lineages defined by incongruent cpDNA and nDNA loci

Medina et al., 2019; Yu et al., 2013). In these conditions, we further suggest that the hypothesis of niche similarity should be tested among trans-oceanically disjunct populations before the data are combined in a single model.

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DATA AVAILABILITY STATEMENT

The occurrence records used to calibrate and evaluate SDMs are provided in Appendix S1.

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BIOSKETCH

FC is a PhD student whose doctoral research focuses on the ecological, biotic and evolutionary factors shaping the segregation of bryophyte communities along an elevation gradient in the context of climate change.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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3. Chapter II

Macroclimatic structuring of spatial phylogenetic turnover in liverworts

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Abstract

Phylogenetic turnover has emerged as a powerful tool to identify the mechanisms by which biological communities assemble. When significantly structured along environmental gradients, phylogenetic turnover evidences phylogenetic niche conservatism, a critical principle explaining patterns of species distributions at different spatio-temporal scales. Here, we quantify the contribution of geographic or macroclimatic drivers to explain patterns of phylogenetic turnover in an entire phylum of land plants, namely liverworts. We further determine whether climatic niche conservatism has constrained the distribution of liverworts in the course of their evolutionary history. Two datasets, one insular, focused on 60 archipelagos and including 2346 species, and the second global, including 6334 species in 451 oceanic and continental Operational Geographic Units (OGUs) worldwide, were assembled. Phylogenetic turnover among OGUs was quantified through π_{st} statistics. π_{st}-through-time profiles were generated at 1 myr intervals along the phylogenetic time-scale and used to compute the correlation between π_{st}, current geographic distance and macroclimatic variation with Mantel tests based on Moran spectral randomization to control for spatial autocorrelation. The contribution of macroclimatic variation to phylogenetic turnover was about four-times higher than that of geographic distance, a pattern that was consistently observed in island and global geographic settings, and with datasets including or excluding species-poor OGUs. The correlation between phylogenetic turnover and geographic distance readily decayed at increasing phylogenetic depth, whereas the

relationship with macroclimatic variation remained constant until 100 mya. Our analyses reveal that changes in the phylogenetic composition among liverwort floras across the globe are primarily shaped by macroclimatic variation. They demonstrate the relevance of macroclimatic niche conservatism for the assembly of liverwort floras over very large spatial and evolutionary time scales, which may explain why such a pervasive biodiversity pattern as the increase of species richness towards the tropics also applies to organisms with high dispersal capacities.

Keywords: biogeography, environmental filtering, spatial phylogenetic turnover, phylogenetic niche conservatism, phylogenetic scale, bryophytes

Introduction

Disentangling the contribution of ecological factors and geographic isolation on the spatio-temporal assembly of biological communities has long been a major focus in ecology and evolutionary biology (Segovia et al. 2020). The definition of the world's biogeographic regions, which dates back to Wallace's (1876) seminal work entitled 'The Geographical Distribution of Animals', reflects the isolation of lineages as a result of historical factors, such as plate tectonics and dispersal limitations, and their subsequent diversification across major environmental gradients (Holt et al. 2013). In organisms with higher dispersal capacities, and plants in particular, plate tectonics conversely played a very limited role for diversification (Sanmartin and Ronquist 2004), which primarily takes place following long-distance dispersal within the same macro-environmental niche (Crisp et al. 2009, Gagnon et al. 2018).

Phylogenetic turnover, which quantifies the phylogenetic distance among species within and among communities (Graham and Fine 2008), is precisely affected by two main macroecological and evolutionary processes. On the one hand, trans-oceanic disjunct communities are expected to display higher average interspecific phylogenetic divergence between, versus within, continents, if speciation occurs at a faster rate than inter-continental migration (Hardy et al. 2012). On the other hand, the niche conservatism hypothesis posits that species sharing the same niche should, on average, be more phylogenetically related to each other than pairs of species from different niches, creating significantly higher phylogenetic turnover between than within habitats (Graham and Fine 2008, Segovia et al. 2020). Therefore, phylogenetic niche conservatism can be detected when the distribution of ecological traits matches both species distributions and evolutionary relationships (Losos 2008), i.e., when phylogenetic turnover and environmental variation are significantly correlated (Jin et al. 2015).

While contemporary geographic and environmental filtering may hence have left an imprint on patterns of taxonomic and phylogenetic turnover, its effect may, however, be perceived only at certain depths along the phylogenetic time-scale (Duarte et al. 2014, Mazel et al. 2017). For example, two regions may not share any species, but if their species all belong to the same higher taxonomic units due to, for instance, strong phylogenetic niche conservatism, then the phylogenetic turnover between these two regions will be 0 at that taxonomic level. The phylogenetic scale used to define the structure of ecological assemblages may therefore also influence the relationships between phylogenetic patterns and environmental gradients depending on the degree of phylogenetic niche conservatism (Wiens and Graham 2005).

Here, we analyse phylogenetic turnover and its geographic and environmental drivers at different phylogenetic levels within an entire phylum of land plants, the Marchantiophyta or liverworts, which include about 7,500 species (Söderström et al. 2016). Following sexual reproduction, they disperse via spores, which are smaller than those of ferns and smaller than angiosperm seeds. Liverworts, and bryophytes in general, thus exhibit high long-distance dispersal capacities that erode any signal caused by geographic isolation, as evidenced by their strikingly low rates of endemism (Söderström 1996, Patiño and Vanderpoorten 2018), skewed presence-per-k-island curves (Söderström 1996), the high frequency of trans-oceanic disjunct distributions (Patiño and Vanderpoorten 2018), and flatter species-area relationships compared to angiosperms (Patiño et al. 2014). As a result, similar levels of bryophyte species richness have been reported in island and continental settings (Patiño et al. 2015a). On oceanic islands, models reflecting environmental heterogeneity therefore explain species richness patterns better than more complex models integrating time and connectivity (Patiño et al. 2013a). Altogether, these observations raise the hypothesis that phylogenetic turnover is better explained by environmental filters than by geographic isolation. Recent studies in specific lineages of mosses, the sister group to liverworts (Wickett et al. 2014), revealed significant niche conservatism (Johnson et al. 2015, Piatkowski & Shaw 2019), but the relevance of this mechanism in shaping species distribution patterns at broad spatial and phylogenetic scales, and in different geological settings, has not been assessed yet. More specifically, we address the following questions:

- Is spatial phylogenetic clustering among liverwort floras significant, i.e., is the observed phylogenetic turnover higher than that expected following randomization of the phylogenetic relationships among species? If so, to what extent is it explained by geographic distance and/or macroclimatic variation, pointing to large-scale macroclimatic niche conservatism? Given the high long-distance dispersal capacities of the group, we hypothesize that macroclimatic variation is a better predictor of phylogenetic turnover than geographic distance, evidencing macroclimatic niche conservatism (H1).
- How did the correlation between phylogenetic turnover, geographic distance and macroclimatic variation evolve through time? Due to the high long-distance dispersal capacities of liverworts, the number of range disjunctions should quickly increase with taxonomic rank, decoupling phylogenetic and geographic distances. We therefore hypothesize that any signal of a correlation between phylogenetic turnover and geographic distance should rapidly erode with increasing evolutionary time (H2). By contrast, if liverwort diversification has been constrained by macroclimatic conservatism during their evolutionary history, the explanatory power of contemporary macroclimatic variation on phylogenetic turnover is expected to persist over large evolutionary time-scales (H3).

Material and methods

Data sampling

The world checklist of liverworts (Söderström et al. 2016) served as a taxonomic basis to standardize species names and higher taxonomic ranks across reference sources and filter out all species with ‘serious doubts’ (915 species). We scored species distributions in Operational Geographic Units (OGUs) from the most comprehensive database of liverwort species distributions available to date, which combines existing data on nomenclature, taxonomy and distribution, and has been built in the context of the Early Land Plants Today project (Söderström et al. 2020). The checklist and distribution data are derived from a working

database centralizing nomenclature, taxonomy and geography on a global scale. As of January 2019, the database included about 39,000 names of about 8,600 'accepted' taxa, a bibliography of more than 11,000 references and more than 1,000,000 distribution records. Since, unlike in higher plants, introductions of bryophytes species are very rare (Mateo et al. 2015), complete species lists were employed. Although we did not enforce a constraint on the minimum number of species per OGU, as we tested the impact of species richness on the results (see below), we ensured that the checklists were sufficiently complete, i.e., that the number of reported species fell into a reasonable range for the given biome and area. In arid areas such as the Sahel for instance, many OGUs include a very low liverwort species richness, primarily comprised of complex thalloid liverworts (Wigginton 2018).

Our sampling primarily focused on oceanic archipelagos for two main reasons. First, they represent naturally circumscribed OGUs. Second, having never been connected to any landmass, they offer an ideal context for addressing the question of geographic isolation, as they are surrounded by an unsuitable matrix for potential colonisers, rendering long-distance dispersal mandatory (Whittaker and Fernandez-Palacios 2007). Since the islands of a same archipelago share the same geological history, they cannot be considered as independent sampling units (Bunnefeld and Phillimore 2012). As recommended by Santos et al. (2010) for large-scale macroecological studies, entire archipelagos instead of single islands were therefore employed as OGUs to avoid pseudo-replication issues. Altogether, the distributions of 2346 liverwort species were reported from 60 archipelagos world-wide (hereafter, the 'archipelago' dataset (Fig. S1)). Species richness per archipelago ranged between 2 and 400 species (Table S1).

Because oceanic islands are geographically isolated, the distance separating them from continental sources acts as a filter for potential migrants (Whittaker and Fernandez-Palacios 2007), and consequently island biota typically differ from continental ones. This phenomenon, termed island disharmony (König et al. 2021), affects the patterns of beta diversity between island and continental biota (Stuart et al. 2012, König et al. 2017). We therefore analysed a second dataset (hereafter, the 'global' dataset) composed of 6334 liverwort species from 451 OGUs world-wide (Fig. S1). For practical reasons, these OGUs were mostly defined based on political limits. Species richness per OGU ranged between 2 and 820 species (Table S1).

We investigated the impact of the inclusion of species-poor OGUs and repeated the analyses twice, first with all OGUs included ('full' dataset), second with only OGUs harboring >10 species ('reduced' dataset). The reduced archipelago and global datasets included 2344 species x 51 OGUs and 6333 x 415 OGUs, respectively.

Finally, we investigated variation among the four major lineages of liverworts: (i) the Marchantiopsida (or complex thalloids); the Jungermanniopsida (or leafy liverworts), further divided into (ii) Porellales and (iii) Jungermanniales; and (iv) the simple thalloids (Metzgeriidae + Pelliidae) (Söderström et al. 2016). Globally, complex thalloids tend to be ground-dwelling. They include genera that rarely produce specialized asexual diaspores, but fairly large spores. For instance, the spores of *Riccia*, the most speciose genus of complex thalloids, typically range between 50 and 100 µm, and are produced within a capsule that is embedded within the thallus, thereby limiting dispersal capacities, but enabling the species to thrive in harsh environments, such as soil crusts (Rosentreter and Root 2019). By contrast, leafy liverworts tend to be much more sensitive to drought, and can sometimes produce both specialized asexual diaspores and comparatively smaller spores. Leafy liverworts can further be divided into two main groups, namely the Porellales, which include the vast majority of epiphytic lineages, and the Jungermanniales, which tend to be primarily terricolous.

The centroid of each OGU was determined in QGIS v.3.14.1 (QGIS development Team 2020) with shapefiles from GADM v. 3.6 (gdam.org). A geographic distance among the centroids of each pair of OGU was computed in R v.4.0.2 (R Core Team 2020) with the package raster (Hijmans 2020). To characterize each OGU macroclimatically, 19 bioclimatic variables at a resolution of 30 arcseconds were downloaded from Chelsa v.2.1 (Karger et al. 2017, 2018). Although the investigated OGUs, and archipelagos in particular, may experience substantial climatic variation across their range, we summarized this variation by the average value across pixels, assuming that, given the worldwide scale of the geographic framework, this average would sufficiently characterize the differences in macroclimatic conditions among OGUs. Subsequent analyses were performed at the level of each macroclimatic variable individually. We also generated a compound, synthetic macroclimatic variable by standardizing each variable and implementing them in a principal component analysis (PCA) with the package ade4 (Bougeard and Dray 2018). The two first principal components, accounting for 77% of the total variance, were kept to generate a matrix of Euclidian climatic distance between each pair of OGUs. Wind connectivity, which has been shown to account for present distribution patterns in spore-producing plants on islands (Muñoz et al. 2004), was not investigated here. In fact, the underlying hypothesis that we test is that phylogenetically closely related species are more likely to occur (i) under similar climatic conditions due to niche conservatism and (ii) in geographically close areas due to dispersal limitations. Since wind patterns substantially vary over short periods of thousands of years, i.e., much less than the timeframe of speciation processes, we assume that present-day wind conditions are unlikely to affect the phylogenetic structure of liverwort floras.

Phylogenetic information was derived from the chronogram of the Liverwort Tree of Life, which is based on the analysis of eight genes from all genomic compartments, includes 303 genera representing 84% of the total extant generic diversity, and is to date the taxonomically and molecularly most densely sampled phylogeny of liverworts (Laenen et al. 2014). Since the phylogeny includes a single species per genus, all congeneric species included in the distribution database were grafted onto the genus-level phylogeny, ensuring that phylogenetic relationships and branch lengths within genera were random and that the ages of genus crown nodes ranged between time present and the age of their stem node. Species that belong to an unsampled genus (162 species) were deleted from the analyses. 100 trees with randomly resolved relationships among congeneric species were then generated and analyzed as described below to take phylogenetic uncertainty into account.

Data analysis

Phylogenetic turnover in relatedness of species (or higher taxa) among sites (hereafter, phylogenetic turnover, Miller et al. 2017) was quantified through the π_{st} statistics (Hardy 2008, Hardy et al. 2012) as implemented by Spacodi (Hardy 2010). π_{st} is defined as 1 – *MPDw*/*MPDa*. MPDw and MPDa represent the mean divergence time between distinct species sampled within and between OGU, respectively:

$$MPDw = 1/N \sum_{k} \left(\sum_{i} \sum_{j \neq i} \delta_{ij} P_{ik} P_{jk} \Big/ \sum_{i} \sum_{j \neq i} P_{ik} P_{jk} \right)$$

$$MPDa = 1/N\,(N-1) \sum_{k} \sum_{l \neq k} \frac{\sum_i \sum_{j \neq i} \delta_{ij} P_{ik} P_{jl}}{\sum_i \sum_{j \neq i} P_{ik} P_{jl}}$$

N is the total number of OGUs. Since we only considered pairwise measures, *N* = 2 here. δ_{ij} is the divergence time between species *i* and *j*, P_{ik} = 1 if species *i* occurs in OGU *k*, otherwise P_{ik} = 0 and similarly for P_{jl} for species *j* in OGU *l*.

A positive π_{st} indicates that species co-occurring in the same OGU are, on average, more related than species sampled among OGUs, reflecting a spatial phylogenetic turnover between OGUs. π_{st} is negative when species are less related within, than between, OGUs, which may result from biotic interactions. To test the hypothesis that $\pi_{st} > 0$, 100 π_{st} values were generated from each of the 100 phylogenies (thus for a total of 10,000 π_{st} values) whose species were randomized among the tips to build the distribution of the null hypothesis, and then compared to the observed π_{st} values.

The correlation between π_{st}, geographic distance (and its log-transformation) and macroclimatic variation was computed through partial Mantel tests. Significance was tested by 999 permutations with the package vegan (Oksanen et al. 2019). Because standard permutation procedures of regular Partial Mantel tests largely fail to actually control for spatial autocorrelation (Guillot and Rousset 2013), we implemented the procedure described by Crabot et al. (2019) with the packages ade4 (Bougeard and Dray 2018), adespatial (Dray et al. 2020) and spdep (Bivand and Wong 2018). This procedure is based on Moran spectral randomization, preserving the spatial structures of the original variables so that spatial autocorrelation is taken into account, avoiding the issue of inflated correlations and type I error rates associated with regular Partial Mantel tests.

To investigate the variation of π_{st} through time, we generated π_{st}-through-time profiles, analogous to the β-diversity through time framework (Groussin et al. 2017) at 1 myr intervals along the phylogenetic time-scale. To this end, the phylogenetic tree was pruned to the desired depth by collapsing all descendent leaves of each of the branches encountered at 1 myr periods, so that the branch lengths leading to these new terminal nodes progressively shortened. The geographic distribution of these branches was calculated as the union of the distributions of their descending leaves. Importantly, as Mazel et al. (2017) highlighted, this approach does not intend to estimate the ancestral geographic range of these branches, but simply the current extent of their geographic distribution at that phylogenetic level. Furthermore, while our π_{st} through-time analyses thus incorporates phylogenetic information, they also have limitations inherent to phylogenies themselves. In particular, they do not explicitly account for extinctions (Mazel et al. 2017). Since species with narrow climatic niches and/or low dispersal capacities could potentially be more prone to extinctions, failure to incorporate extinctions could bias the correlation analysis between π_{st} and climatic and geographic drivers among communities that progressively become dominated by species characterized by high dispersal capacities and wide climatic ranges. The fact, that we observed significant correlations between π_{st} and climatic variation through time, and also, in some lineages, with geographic distance (see below), suggests, however, that extinctions did not completely erode the relationships between π_{st}, geographic and environmental drivers.

To help visualizing whether broad climatic niche preferences are conserved at high taxonomic levels, we calculated for each species of the global dataset a 'tropicality index' (Appendix 1) as the proportion of its latitudinal range that falls within the tropics, circumscribed by the 23.5° latitude parallels (Economo et al. 2018; Rabosky et al. 2018), minus the proportion of the latitudinal range that falls within extratropical areas. This produces a continuous measure from −1 (extratropical only) to 0 (one-half extratropical, one-half tropical) to 1 (tropical only) (Kerkhoff et al. 2014). We derived the most likely sets of ancestral states under a Brownian motion model as implemented by the fastAnc function in the R package phytools (Revell 2012). The analysis was performed on one of the 100 randomly resolved trees at the species level as we focused on the evolution of the tropicality index at the level of the earliest branches.

Finally, we explored whether other metrics of phylogenetic turnover than p_{st} would return similar results. Among these metrics, the PhyloSor index (Swenson 2011) has been widely used in recent analyses

of phylogenetic community structure (Qian et al. 2013, Jin et al. 2015, Segovia et al. 2020). PhyloSor sums the total branch length of shared clades between sites relative to the sum of branch lengths of both sites. PhyloSor can be further split, like taxonomic beta diversity, into two separate components accounting for 'true' phylogenetic turnover ($PhyloSor_{Turn}$) and phylogenetic diversity gradients ($PhyloSor_{PD}$), respectively (Leprieur et al. 2012). PhyloSor and its components, generated with the R package betapart (Baselga et al. 2020), were correlated to geographic distance and macroclimatic variation using the full 'archipelago' dataset.

Results

Phylogenetic turnover among liverwort floras, as expressed by pairwise π_{st} among OGUs, was significantly higher than 0 ($p<0.001$ in all pairwise comparisons across the 100 phylogenetic trees) for both the global and archipelago datasets. Partial Mantel tests revealed low (r=0.08 on average across trees), but significant correlations between phylogenetic turnover and geographic distance for the archipelago dataset (Fig. S2), but not for the global dataset (Table 1). Phylogenetic turnover was also significantly correlated with macroclimatic variation, as expressed by the first two axes of a PCA of 19 bioclimatic variables. After correction for spatial autocorrelation using Moran spectral randomization, average r values reached 0.35 and 0.36, i.e., more than four times higher than with geographic distance, with the archipelago and global dataset, respectively (Table 1). These correlations increased to an average of r=0.55 and 0.41 for the archipelago and global dataset, respectively, in analyses based on 'reduced' datasets including OGUs with >10 species (Table 1). Similar results were obtained with analyses based on phylogenetic beta diversity (PhyloSor), with significant correlation between the turnover component of the latter ($PhyloSor_{Turn}$) and geographic distance and macroclimatic variation, but not with its nestedness component ($PhyloSor_{PD}$) (Table S2).

Table 1. Average (± S.D. across 100 trees, for which species relationships within each genus were randomized) correlation coefficients *r* and associated p-values between the phylogenetic turnover π_{st} of liverwort floras among oceanic archipelagos (n=60) and among OGUs of a global dataset of both oceanic and continental OGUs (n=451) and (i) the logarithmic geographic distance and (ii) macroclimatic variation (as expressed by the first two axes of a PCA of 19 bioclimatic variables, see Table S3 for correlations with each variable independently) using partial Mantel tests implementing Moran spectral randomization to control for spatial autocorrelation. 'Full' and 'reduced' correspond to datasets with all OGUs included and only OGUs with >10 species, respectively.

	***r*±S.D.**	
Archipelago dataset		
	Full dataset	Reduced dataset
Geographic distance	0.08±0.001 p<0.01	0.12±0.001 p<0.01
Macroclimatic variation	0.35±0.004 p<0.01	0.55±0.003 p<0.01
Global dataset		
	Full dataset	Reduced dataset
Geographic distance	$-0.02 \pm 4\ 10^{-4}$ p>0.05	-0.02 ± 10^{-4} p>0.05
Macroclimatic variation	$0.36 \pm 2\ 10^{-3}$ p<0.001	0.41±0.001 p<0.01

Analyses at the level of each of the 19 investigated bioclimatic variables showed the same trends (Table S3). Temperature-related variables were more frequently significantly correlated (seven out of 11 variables), and exhibited higher correlation coefficients (*r*=0.24 on average, up to 0.36 for annual mean temperature, minimum temperature of coldest month, mean temperature of wettest quarter, and mean temperature of coldest quarter) than precipitation-related variables (*r*=0.08 on average, up to 0.21 for precipitation seasonality, the only one of the seven precipitation-related variables significantly correlated with phylogenetic turnover). These correlations varied substantially among the main lineages of liverworts (Table 2), as phylogenetic turnover was significantly correlated with geographic distance for the Jungermanniales, but not for the other lineages. Regarding macroclimatic variation, the correlation was highest in leafy liverworts, and absent in simple thalloids.

The relative effect of geographic distance and macroclimatic variation on phylogenetic turnover through a phylogenetic time-scale is shown in Fig. 1 and Fig. S3 for the archipelago and global datasets, respectively. The correlation between phylogenetic turnover and geographic distance rapidly reaches non-significance (Fig. 1a, S3a). In turn, the contribution of macroclimatic variation to phylogenetic turnover remains fairly constant and significant until about 100 mya (Fig. 1b, S3b). In fact, reconstructions of the

'tropicality index' (Fig. S4) graphically illustrated that tropical and extra-tropical lineages tend to be phylogenetically clustered.

Table 2. Average (±S.D. across 100 trees, for which species relationships within each genus were randomized) correlation coefficients *r* and associated p-values between the phylogenetic turnover π_{st} between the floras of the four major liverwort clades (Porellales and Jungermanniales composing the leafy liverworts) among oceanic archipelagos (n=60) and (i) the logarithmic geographic distance and (ii) macroclimatic variation (as expressed by the first two axes of a PCA of 19 bioclimatic variables using partial Mantel tests implementing Moran spectral randomization to control for spatial autocorrelation.

Clade	Geographic distance	Macroclimatic variation
Complex thalloids	0.020±0.005 p>0.05	0.27±0.02 p<0.05
Simple thalloids	0.050±0.010 p>0.05	-0.02±0.02 p>0.05
Leafy liverworts	0.01±0.001 p>0.05	0.51±0.003 p<0.01
Porellales	-0.024±0.004 p>0.05	0.31±0.10 p<0.01
Jungermanniales	0.25±0.004 p<0.01	0.29±0.003 p<0.01

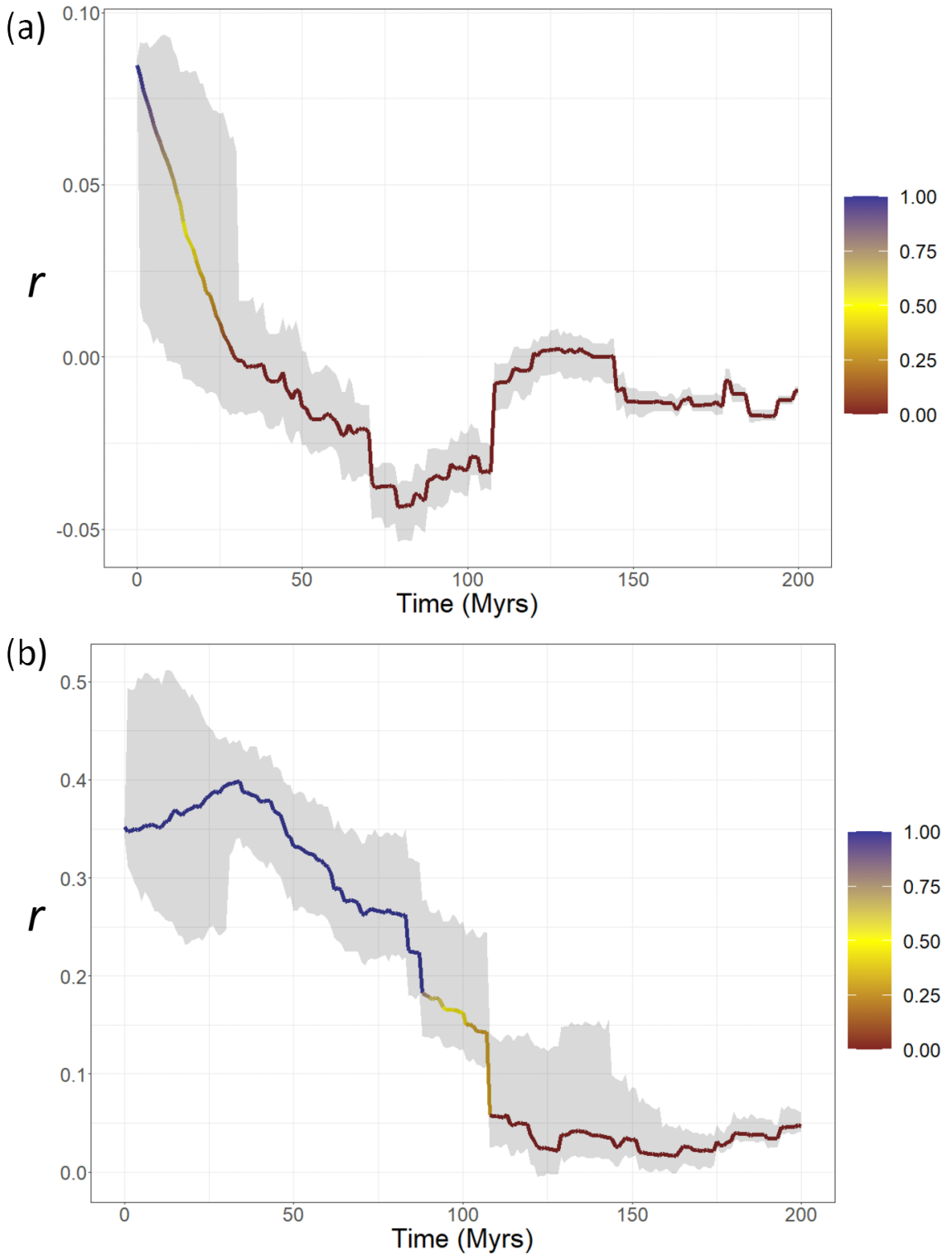

Fig. 1. Relative effect, as expressed by the correlation coefficient *r* of a partial Mantel test, of (a) geographic distance and (b) macroclimatic variation, as expressed by the first two axes of a PCA of 19 bioclimatic variables, following Moran spectral randomization to control for spatial autocorrelation on phylogenetic turnover in oceanic archipelago liverwort floras through a phylogenetic time-scale. Lines and grey ribbons represent, at 1 myr intervals, the mean correlation coefficient and its minimum-maximum range, respectively, across 100 trees, for which species relationships within each genus were randomized. The color gradient shows the percentage of significant correlations at the 0.05 level and ranges between 0 (red) and 100% (blue) of significant correlations across 100 trees.

Discussion

Phylogenetic turnover of liverwort communities revealed significant correlations with macroclimatic conditions, independently from geographic distance, adding to emerging evidence for the role of environmental filtering on community assembly through time (Saladin et al. 2019, Segovia et al. 2020). These correlations were observed with two different metrics of phylogenetic turnover, π_{st} and PhyloSor. The fact that the 'true' turnover of PhyloSor, and not its nestedness component, is correlated with macroclimatic variation, suggests that the patterns observed are not caused by phylogenetic diversity gradients, but by a true phylogenetic turnover among communities. The correlation between phylogenetic turnover and macroclimatic variation is evidence for niche conservatism shaping macroclimatic niche preferences at a world scale, reinforcing the idea that biome conservatism is a primary driver of present-day distribution patterns of biodiversity (Crisp et al. 2009, Segovia et al. 2020). Evidence for phylogenetic conservatism of microhabitat conditions is mounting in bryophytes (Johnson et al. 2015, Piatkowski & Shaw 2019), and we demonstrate here the significance of this mechanism for also shaping large-scale patterns of liverwort assemblage distributions. Phylogenetic niche conservatism of macroclimatic factors is further illustrated by the phylogenetic clustering of the 'tropicality index'. Although further analyses based on actual measures of the phylogenetic signal present in climatic niche traits would be necessary, these results suggest that the evolution of macroclimatic niches is evolutionary constrained, as if they were heritable.

Despite the fact that oceanic island biota have been pre-filtered upon colonization depending on their dispersal capacities, causing differences of beta diversity patterns of angiosperms and vertebrates in island and continental settings (Stuart et al. 2012, König et al. 2017), phylogenetic turnover was also correlated with geographic distance with the oceanic archipelago dataset, but not the global one. This result is, at first sight, surprising because island species must have had, at least upon colonization, high dispersal capacities, potentially erasing any signal of geographic isolation in patterns of phylogenetic turnover. Congruently with the idea that island species have been filtered depending on their dispersal capacities, a bias towards bisexuality was reported in island bryophytes and interpreted as a result of the higher capacity of bisexual species than unisexual ones to produce spores, which are supposedly more prone to long-distance dispersal, and hence, to reach remote islands (Patiño et al. 2013b). The idea, that bisexual species exhibit larger ranges than unisexual ones has, however, been challenged (Laenen et al. 2016) and in fact, the low, but significant signal of geographic isolation observed among oceanic archipelago floras in liverworts vanished in the analyses of the global dataset. Although oceans are not a major impediment for diaspore dispersal, as evidenced by overlapping slopes of isolation-by-distance curves in populations separated by an identical distance above continents and oceans (Hutsemekers et al. 2011, Kyrkjeeide et al. 2016), we interpret the presence of a geographic signal on patterns of phylogenetic turnover in oceanic archipelagos in terms of the true geographic isolation from any potential source of the latter.

The observed correlations between phylogenetic turnover and climatic drivers lay in the range of the few previous studies addressing similar questions in vascular plants (e.g., correlation coefficients of 0.4 and 0.2 were reported between climatic variation and phylogenetic turnover in angiosperm floras across China (Qian et al. 2020) and in tropical rainforests (Hardy et al. 2012), respectively). Although higher correlations, up to 0.5, were observed in the present study between phylogenetic turnover and climatic and geographic distance when species-poor OGUs were removed, the analysis of the full and reduced datasets, using two very different datasets in terms of numbers of OGUs and geographic context, revealed identical patterns. This strengthens the robustness of our conclusions and reinforces the idea that π_{st}, as a measure

of the ratio between the average phylogenetic distance among species within vs among OGUs, is reasonably robust to differences in species richness among OGUs (Hardy et al. 2012). We suggest that the large fluctuations of the π_{st} statistic reported by Ives and Helmus (2010) in small communities were caused, at least in part, by their redefinition of this statistic, so that the mean inter community phylogenetic distance includes pairwise comparisons between pairs of identical species, which departs from the original definition by Hardy and Senterre (2007). The robustness of p_{st} to differences in species richness among OGUs makes it unnecessary to define an arbitrary threshold for selecting OGUs included in the analysis. By contrast, other metrics such as PhyloSor, which includes a phylogenetic species richness component ($PhyloSor_{PD}$), should be sensitive to variations of species richness among OGUs, and hence, of the completeness of the species inventory of the OGUs.

Most importantly, phylogenetic turnover is four times less strongly correlated with geographic distance than with climatic variation. These results contrast with those reported for birds and mammals (Mazel et al. 2017), wherein contemporary geographic distances explain beta diversity better than climate, suggesting that dispersal limitations in these lineages have a greater influence on phylogenetic turnover than climatic filtering, which is in line with the idea that, at the global scale, faunas of different continents exhibit striking differences due to ancient geographic isolation associated with plate tectonics. Within continents, recent analyses in angiosperms suggest that tree lineages tend to retain their ancestral environmental relationships and that phylogenetic niche conservatism is the primary force structuring their distributions (Qian et al. 2020, Segovia et al. 2020). In line with the fact that contemporary ecological factors prevail over factors associated with dispersal limitations, such as island age and geographic isolation, to explain patterns of species richness in island bryophytes (Sundberg et al. 2006, Patiño et al. 2013a, Aranda et al. 2014, Tiselius et al. 2019, Torre et al. 2019), the present results also suggest that macroclimatic filters play a much more important role than dispersal limitations in the assembly of liverwort floras, emphasizing the prevalence of macroclimatic variation over geographic distance for shaping pattern of phylogenetic turnover in plants in general (Qian et al. 2020) across large geographic scales.

Major lineages of liverworts substantially differ, however, in their response to macroclimatic and geographic variation. The absence of correlation between phylogenetic turnover and geographic distance was expected in the Porellales, which include the bulk of the diversity of epiphytic liverworts, a condition that substantially impacts on spore height release, and thus dispersal capacities (Zanatta et al. 2020). By contrast, geographic distance significantly accounted for phylogenetic turnover in Jungermanniales, but not in the complex thalloids, despite a series of life-history traits in the latter that, at first sight, do not promote dispersal. In fact, although molecular work would be needed to control for potential cryptic diversification, some complex thalloids exhibit striking amphitropical ranges, potentially achieved by bird-mediated dispersal of their mostly bisexual spores (Gradstein 2017). Finally, in line with the globally higher ability of thalloid liverworts to thrive in harsh environments, phylogenetic turnover of thalloid lineages did not or only weakly correlate with macroclimatic variation, whereas the highest correlations between phylogenetic turnover and macroclimatic variation were observed in the more drought-sensitive leafy liverworts.

Interestingly, analyses performed at the level of individual climatic variables revealed that liverwort phylogenetic turnover was better correlated with temperature than precipitation, a pattern that was at first sight unexpected in liverworts due to the reliance of the latter on rainfall for water uptake, making them prime indicators of climate change (He et al. 2016). Given the very large scale of the present study, this result should, however, be interpreted with caution, because the relative contribution of climatic drivers to

beta diversity may differ between latitudinal and altitudinal gradients, and among biogeographic regions (Tang et al. 2012).

Congruent with our second hypothesis, the correlation between phylogenetic turnover and geographic distance readily decays with increasing phylogenetic depth. By contrast, the explanatory power of contemporary macroclimatic variation on phylogenetic turnover only slightly decreases towards deep branches and becomes insignificant only beyond 100 myrs, pointing to the crucial role of climatic niche conservatism for the assembly of liverwort assemblages over very large evolutionary time scales. Such a persistence of the importance of macroclimatic factors for explaining large-scale distributions of high-level taxa, recently evidenced in angiosperms (Kusumoto et al. 2021), is, at first sight, more striking in liverworts, whose genera and higher-level taxa tend to be broadly distributed worldwide. Nevertheless, even widely distributed taxa are not necessarily equally distributed across regions. For example, *Lejeunea* and Lejeuneaceae are sub-cosmopolitan, but originated in tropical areas, where they are still much more widely distributed today (Lee et al. 2020). In fact, reconstructions of the 'tropicality index' show that broad climatic niche preferences of liverworts are largely conserved over large evolutionary time-scales, accounting for the persistence of the correlation between phylogenetic turnover of higher taxa and climatic variation reported here.

Our results thus lend support to the idea that contemporary geographic and climatic distances do not impact beta diversity patterns at the same phylogenetic time-scale (Mazel et al. 2017, Roy et al. 2019). They contrast, however, with previous reports in mammals and birds, wherein contemporary geographic distances explain the ß-diversity of deep branches better than the ß -diversity of shallow branches, whereas climatic distances explain the ß -diversity of species better than that of deep branches (Mazel et al. 2017). Such a discrepancy suggests that, while mammals and birds first diversified in geographic isolation due to either plate tectonics or rare long-distance dispersal events and then across climatic gradients within large continental areas, liverworts diversified primarily through time along macroclimatic gradients. A signature of geographic isolation can only be found at the level of the shallowest branches, as species may not have had the time yet to disperse across long distances. In turn, the sharp decrease of the correlation between macroclimatic variation and phylogenetic turnover 100 mya can be interpreted in terms of a burst of diversification (Laenen et al. 2014), especially obvious at the level of epiphytic lineages (Feldberg et al. 2014), triggered by the development of large, humid megathermal angiosperm forests, after which lineage diversification would have been constrained macroclimatically.

Our results have several consequences. First, evidence for macroclimatic niche conservatism at shallow phylogenetic depths lends support to the application of Species Distribution Models, which are among the most widely used tools in ecology (Araujo et al. 2019), but rely on the assumption of niche conservatism for model projection at different spatial and temporal scales (Wiens et al. 2009).

Second, the very weak contribution of geographic distance on phylogenetic turnover may explain why so few bryophyte species are invasive, because virtually all species would have already colonized their climatically suitable range. In turn, the relationship between phylogenetic turnover and macroclimatic variation suggests that bryophyte invasions are constrained by the availability of suitable climates in the invaded range. The observed signal for climatic niche conservatism in fact suggests that alien species may not have the ability to shift niche, as further evidenced by the absence of any signal of niche expansion upon invasion in invasive mosses and liverworts (Mateo et al. 2015).

Third, macroclimatic niche conservatism in liverworts may explain why, even in organisms with high dispersal capacities, such a pervasive biodiversity pattern as the increase of species richness towards the

tropics also applies (Wang et al. 2017), in line with the hypothesis that plant biodiversity is evolutionarily structured globally following a tropical-extratropical pattern (Segovia et al. 2020). While tropical niche conservatism may hence globally limit opportunities for tropical lineages to establish into extratropical regions, this macroclimatic filter is not impermeable, and many tropical lineages have successfully colonized extratropical regions, as illustrated by the reconstruction of the 'tropicality index'. Such 'irradiations' of tropical lineages into extratropical regions can still be found today, as exemplified by the colonization of the western fringe of Europe by lineages of tropical origin (Patiño et al. 2015b), and this recurrent pattern explains the high uncertainty in ancestral area reconstructions in liverworts at and above the genus level (Laenen et al. 2018).

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Data availability. The molecular data sets and phylogenetic trees can be obtained from http://purl.org/phylo/treebase/phylows/study/TB2:S15950?x-access-code=98d94511d8c016de8eae6f21c851826e&format=html. Species distribution data are available from www.catalogueoflife.org/data/dataset/1074.

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Appendix

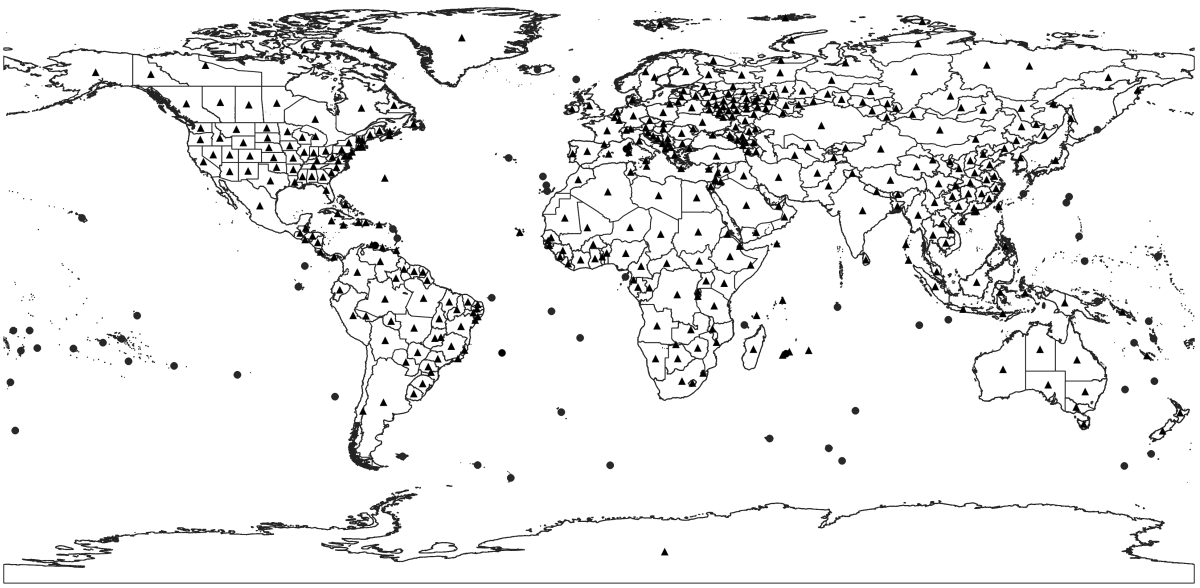

Fig. S1. Location of the 451 Operational Geographic Units (OGUs), including 60 oceanic archipelagos, used to measure phylogenetic turnover among liverwort floras. The centroids of oceanic archipelagos are represented by a circle and those of the remaining OGUs by a triangle.

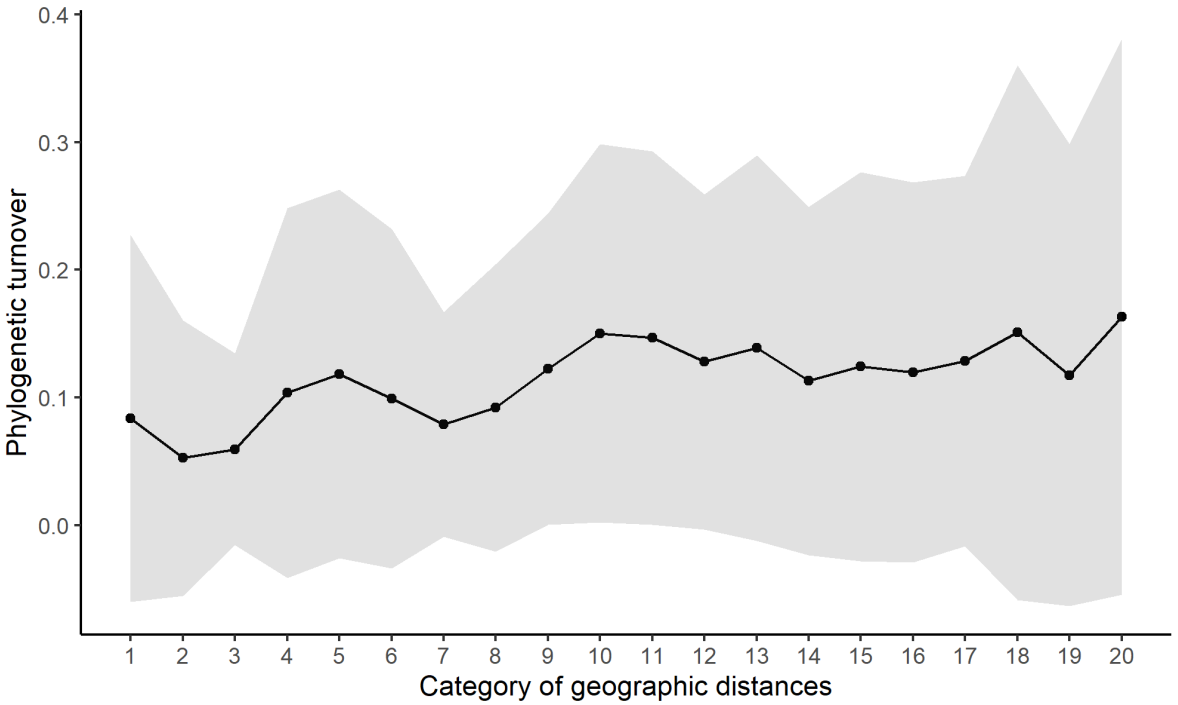

Fig. S2. Spatial autocorrelogram between average (±SD, grey ribbon) π_{st} values between oceanic island liverwort floras per distance class (1000km) and geographic distance.

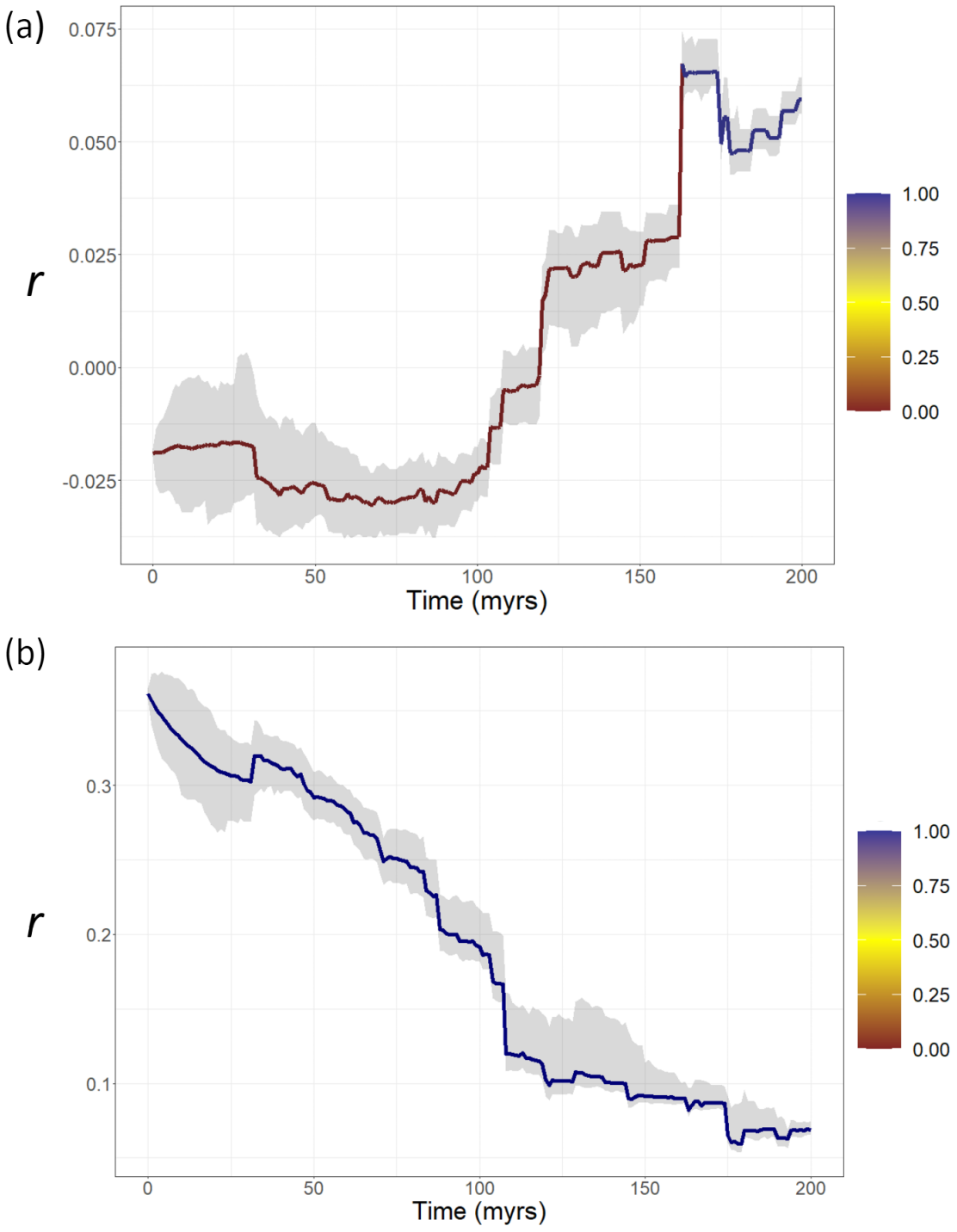

Fig. S3. Relative effect, as expressed by the correlation coefficient *r* of a partial Mantel test, of (a) geographic distance and (b) macroclimatic variation, as expressed by the first two axes of a PCA of 19 bioclimatic variables, following Moran spectral randomization to control for spatial autocorrelation on phylogenetic turnover in the liverwort floras of 451 OGUs worldwide through a phylogenetic time-scale. Lines and grey ribbons represent, at 1 myr intervals, the mean correlation coefficient and its minimum-maximum range, respectively, across 100 trees, for which species relationships within each genus were randomized. The color gradient shows the percentage of significant correlations at the 0.05 level and ranges between 0 (red) and blue (100 %) of significant correlations across 100 trees.

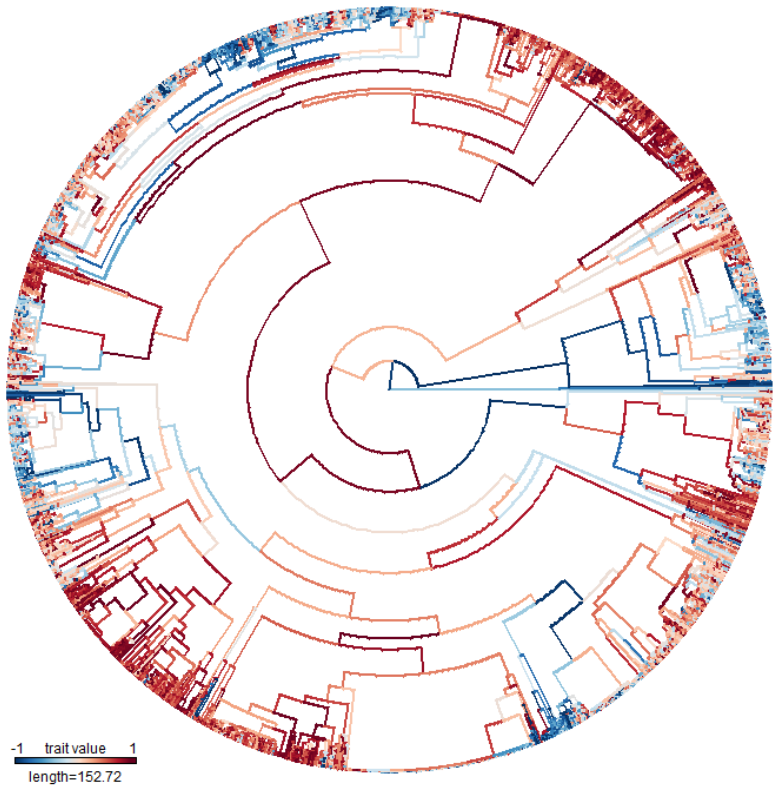

Fig. S4. One of the 100 trees of the liverwort phylogeny randomly resolved at the species level, with branches colored according to the estimated tropicality TI value ranging from red (TI = 1) to blue (TI = –1).

Table S1. List of the Operational Geographic Units and their numbers of liverwort species. (a) Oceanic archipelagos. (b) Global datasets.

(a)

Iceland	137
Azores	154
Canary Islands	139
Cape Verde	44
Madeira	174
Selvagens	4
Guinea Gulf Islands	210
Ascension	23
St Helena	40
Chagos Archipelago	8
Comoros	163
Kuril Is	231
Kazan-retto (Volcano)	43
Nansei-Shoto	249
Ogasawara-shoto (Bonin)	93

Keeling (Cocos) Is	5
Bismarck Archipelago	88
Lord Howe Is	38
Norfolk Is	54
Antipodean Is	181
Chatham Is	51
Kermadec Is	49
Fiji	299
Niue	16
Samoa	200
Santa Cruz Is	5
Tonga	47
Vanuatu	144
Wallis-Futuna Is	5
Cook Is	16
Marquesas	12
Society Is	161
Tuamotu Is	6
Tubuai Is	7
Caroline Is	143
Mariana Is	48
Marshall Is	18
Hawaii	184
C American Pacific Is	96
Leeward Islands	400
Windward Islands	366
Galápagos Is	120
Fernando de Noronha	4
Juan Fernández Is	161
Amsterdam-St Paul Is	31
Bouvet Is	4
Crozet Is	47
Falkland Is	145
Heard-McDonald Is	16
Kerguelen	42
Macquaire Is	46
South Georgia	91
South Sandwich Is	18
Tristan da Cunha	121
Faeroe Islands	125
Easter Is	14
Mascarenes	315

Venezuealan and Netherlands Antilles	19
Asinara	12
Trinidade	17

(b)

Denmark	144
Finland	232
Faeroe Islands	128
Britain	291
Iceland	145
Ireland	232
Norway	274
Svalbard	102
Sweden	259
Austria	261
Belgium	186
Czech Republic	211
Germany	255
Hungary	149
Liechtenstein	101
Luxembourg	133
Netherlands	130
Poland	236
Slovakia	223
Switzerland	255
Andorra	134
Baleares	68
Corsica	148
France	313
Portugal	184
Sardinia	93
Spain	280
Albania	116
Bosnia-Herzegovina	108
Bulgaria	181
Croatia	165
Greece	147
Italy	281
Kosovo	29
Crete	71

Makedonia	100
Malta	26
Montenegro	145
Romania	222
Serbia	132
Sicily	114
Slovenia	164
Turkey in Europe	37
Belarus	93
Estonia	127
Franz Josef Land	40
Kaliningrad	81
Crimea	32
Latvia	127
Lithuania	107
Moldovo	7
Novaya Zemlya	64
Adygea	90
Archangelsk	85
Bashkiriya	99
Belgorod	19
Bryansk	9
Dagestan	50
Karelia	191
Kabardino-Balkaria	86
Karachay-Cherkess	121
Kaluga	41
Kirov	35
Kalmykiya	5
Komi	174
Krasnodar	136
Kursk	23
Leningrad	155
Lipetsk	23
Mari-El	49
Mordoviya	4
Moscow	71
Murmansk	195
Nenets	88
Nizhny Novgorod (Gorkij)	63
Novgorod	44
Orel (Oryol)	31

Orenburg	25
Perm	130
Pskov	78
Penza	7
Rostov	6
Ryazan	29
Samara	15
Severo-Ossetiya	6
Stavropol	11
Saratov	11
Tambov	17
Tatarstan	53
Tula	23
Tver	97
Udmurtiya	28
Ulyanovsk	25
Volgograd	13
Vladimir	27
Voronezh	25
Vologda	102
Yaroslavl	17
Ukraine	181
Algeria	110
Egypt	10
Libya	23
Morocco	99
Tunisia	78
Azores	158
Canary Islands	142
Cape Verde	45
Madeira	179
Benin	21
Gambia	3
Ghana	147
Guinea-Bissau	5
Guinea	80
Ivory Coast	98
Liberia	8
Mali	2
Mauritania	4
Nigeria	144
Niger	17

Senegal	7
Sierra Leone	138
Togo	45
Burundi	97
Central African Republic	58
Cameroon	233
Congo	69
Río Muni	92
Gabon	75
Guinea Gulf Islands	220
Rwanda	253
Zaire	275
Chad	13
Djibouti	9
Eritrea	20
Ethiopia	171
Socotra	33
Somalia	6
South Sudan	2
Sudan	11
Kenya	281
Tanzania	394
Uganda	288
Angola	112
Malawi	221
Mozambique	78
Zambia	65
Zimbabwe	167
Botswana	20
Caprivi Strip	2
Lesotho	91
Namibia	36
South Africa	335
Swaziland	43
Ascension	24
Aldabra	2
Chagos Archipelago	8
Comoros	171
Mauritius	197
Madagascar	430
RÇunion	306
Rodriguez	29

Seychelles	127
Altay krai	145
Altay republic	81
Buryatiya	212
Chelyabinsk	57
Irkutsk	137
Kemerovo	130
Khakassia	10
Khantsi-Mansi	148
Krasnoyarsk	150
Kurgan	2
Novosibirsk	21
Omsk	43
Severnaya Zemlya	51
Sverdlovsk	73
Taymyr	173
Tomsk	74
Tuva	87
Tyumen	53
Yakutiya	204
Yamal-Nenets	165
Zabaykalsky (Chita)	153
Amur	130
Chukotka	186
Jewish	3
Kamchatka	232
Khabarovsk	170
Kuril Is	246
Magadan	108
Primorye	232
Sakhalin	202
Wrangel Island	91
Kazakhstan	22
Kirgizstan	16
Turkmenistan	4
Tadzhikistan	17
Uzbekistan	5
Armeniya	34
Azerbaydzhan	87
Gruziya	169
Afghanistan	23
Cyprus	42

Iran	76
Iraq	11
Israel	44
Jordan	21
Lebanon	49
Palestine	2
Sinai	2
Syria	14
Turkey	180
Oman	17
Saudi Arabia	25
United Arab Emirates	8
Yemen	34
Anhui	179
Chongqing	18
Fujian	237
Gansu	132
Guangdong	192
Guizhou	277
Guangxi	268
Hebei	48
Hainan	260
Heilongjiang	110
Hongkong	146
Hunan	166
Henan	82
Hubei	53
Qinghai	16
Tibet (Xizang)	281
Xinjiang	60
Jilin	155
Jiangsu	41
Jiangxi	187
Liaoning	89
Macau	27
Ningxia	22
Nei Mongol	93
Shaanxi	214
Shandong	86
Sichuan	307
Shanxi	32
Yunnan	602

Zhejiang	288
Mongolia	106
Japan	634
Korea	299
Kazan-retto (Volcano)	44
Nansei-Shoto	256
Ogasawara-shoto (Bonin)	95
Taiwan	527
Bangladesh	56
Bhutan	455
India	820
Kashmir	105
Nepal	427
Pakistan	86
Sri Lanka	328
Andaman Islands	106
Cambodia	138
Laos	67
Burma (Myanmar)	106
Nicobar Is	63
Thailand	489
Vietnam	467
Borneo	671
Keeling (Cocos) Is	5
Java	525
Lesser Sunda Is	117
Malaya	594
Moluccas	318
Philippines	528
Sulawesi	258
Sumatra	457
Bismarck Archipelago	88
New Guinea	801
Solomon Islands	202
Lord Howe Is	41
Norfolk Is	59
New South Wales	358
Northern Territory	40
Queensland	442
South Australia	73
Tasmania	398
Victoria	278

Western Australia	100
Antipodean Is	213
Chatham Is	64
Kermadec Is	53
New Zealand North Is	507
New Zealand South Is	563
Fiji	313
Niue	17
New Caledonia	458
Samoa	208
Santa Cruz Is	5
Tonga	48
Vanuatu	155
Wallis-Futuna Is	5
Cook Is	16
Easter Is	15
Marquesas	12
Society Is	168
Tuamotu Is	6
Tubuai Is	7
Caroline Is	150
Mariana Is	50
Marshall Is	18
Hawaii	192
Alaska	280
Greenland	192
Nunavut	135
Northwest Territories	134
Yukon Territory	132
Alberta	156
British Columbia	267
Manitoba	65
Saskatchewan	42
Labrador	133
New Brunswick	122
Newfoundland	151
Nova Scotia	148
Ontario	158
Prince Edward Island	28
Quebec	216
Colorado	115
Idaho	108

Montana	136
Oregon	173
Washington	205
Wyoming	96
Illinois	115
Iowa	65
Kansas	62
Minnesota	169
Missouri	108
North Dakota	6
Nebraska	30
Oklahoma	64
South Dakota	33
Wisconsin	144
Connecticut	142
Indiana	76
Maine	162
Massachusetts	146
Michigan	164
New Hampshire	164
New Jersey	104
New York	182
Ohio	118
Pennsylvania	128
Rhode Island	84
Vermont	170
West Virginia	118
Arizona	69
California	174
Nevada	51
Utah	64
New Mexico	74
Texas	103
Alabama	113
Arkansas	118
Delaware	55
Florida	168
Georgia	159
Kentucky	111
Louisiana	111
Maryland	88
Mississippi	103

North Carolina	213
South Carolina	136
Tennessee	175
Virginia	152
District of Columbia	64
Mexico	572
Belize	91
Costa Rica	618
C American Pacific Is	100
El Salvador	76
Guatemala	352
Honduras	151
Nicaragua	40
Panama	456
Bermuda	29
Bahamas	42
Cuba	452
Dominican Republic	279
Haiti	119
Jamaica	372
Leeward Islands	418
Netherlands Antilles	16
Puerto Rico	313
Trinidad-Tobago	171
Venezuelan Antilles	4
Windward Islands	383
French Guiana	285
Guyana	311
Surinam	197
Venezuela	723
Bolivia	519
Colombia	812
Ecuador	742
Galápagos Is	125
Peru	672
Acre	120
Alagoas	151
Amazonas	390
Amapá	62
Bahia	368
Ceará	171
Brasília	96

Espírito Santo	293
Fernando de Noronha	4
Goiás	202
Maranhão	90
Minas Gerais	445
Mato Grosso do Sul	113
Mato Grosso	159
Pará	252
Paraíba	100
Pernambuco	248
Piauí	17
Paraná	366
Rio de Janeiro	470
Rio Grande do Norte	33
Rondìnia	58
Roraima	128
Rio Grande do Sul	287
Santa Catarina	304
Sergipe	68
São Paulo	572
Tocantins	32
Argentina	524
Chile	525
Juan Fernández Is	182
Paraguay	78
Uruguay	37
Amsterdam-St Paul Is	35
Bouvet Is	4
Crozet Is	51
Falkland Is	160
Heard-McDonald Is	19
Kerguelen	51
Macquaire Is	54
South Georgia	101
South Sandwich Is	19
Tristan da Cunha	140
Antarctic Island (incl. Antarctic Peninsula, E Antarctica, South Orkney Is., South Shetland Is., and W Antarctica)	35

Table S2. Average (±S.D. across 100 trees, for which species relationships within each genus were randomized) correlation coefficients *r* and associated p-values between phylogenetic beta diversity (PhyloSor) and its two components, phylogenetic turnover ($PhyloSor_{Turn}$) and phylogenetic diversity gradients ($PhyloSor_{PD}$) of liverwort floras ('Full' dataset) among oceanic archipelagos (n=60) and (i) the logarithmic geographic distance and (ii) macroclimatic variation (as expressed by the first two axes of a PCA of 19 bioclimatic variables) using partial Mantel tests implementing Moran spectral randomization to control for spatial autocorrelation.

	Geographic distance	Macroclimatic variation
PhyloSor	0.18±0.005 p<0.01	0.28±0.005 p<0.01
$PhyloSor_{Turn}$	0.26±0.006 p<0.01	0.36±0.010 p<0.01
$PhyloSor_{PD}$	-0.07±0.003 p>0.05	-0.08±0.005 p>0.05

Table S3. Average (the standard-deviation across 100 trees, for which species relationships within each genus were randomized, was systematically <0.01),) correlation coefficients *r* and significance (*: p<0.05 across all trees, p>0.05 across trees otherwise) between the phylogenetic turnover π_{st} of oceanic archipelago liverwort floras and 19 bioclimatic variables using Moran spectral randomization to control for spatial autocorrelation.

Variables	Average *r*
Annual Mean Temperature (bio_1)	0.36*
Mean Diurnal Range (Mean of monthly (max temp - min temp)) (bio_2)	0.01
Isothermality (BIO2/BIO7) (×100) (bio_3)	0.05
Temperature Seasonality (standard deviation ×100) (bio_4)	0.10
Max Temperature of Warmest Month (bio_5)	0.32*
Min Temperature of Coldest Month (bio_6)	0.36*
Temperature Annual Range (BIO5-BIO6) (bio_7)	0.12
Mean Temperature of Wettest Quarter (bio_8)	0.37*
Mean Temperature of Driest Quarter (bio_9)	0.31*
Mean Temperature of Warmest Quarter (bio_10)	0.33*
Mean Temperature of Coldest Quarter (bio_11)	0.36*
Annual Precipitation (bio_12)	0.08
Precipitation of Wettest Month (bio_13)	0.02
Precipitation of Driest Month (bio_14)	0.11
Precipitation Seasonality (Coefficient of Variation) (bio_15)	0.21*
Precipitation of Wettest Quarter (bio_16)	0.02
Precipitation of Driest Quarter (bio_17)	0.11
Precipitation of Warmest Quarter (bio_18)	0.10
Precipitation of Coldest Quarter (bio_19)	-0.03

4. Chapter III

nature COMMUNICATIONS

ARTICLE

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Bryophytes are predicted to lag behind future climate change despite their high dispersal capacities

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The extent to which species can balance out the loss of suitable habitats due to climate warming by shifting their ranges is an area of controversy. Here, we assess whether highly efficient wind-dispersed organisms like bryophytes can keep-up with projected shifts in their areas of suitable climate. Using a hybrid statistical-mechanistic approach accounting for spatial and temporal variations in both climatic and wind conditions, we simulate future migrations across Europe for 40 bryophyte species until 2050. The median ratios between predicted range loss vs expansion by 2050 across species and climate change scenarios range from 1.6 to 3.3 when only shifts in climatic suitability were considered, but increase to 34.7–96.8 when species dispersal abilities are added to our models. This highlights the importance of accounting for dispersal restrictions when projecting future distribution ranges and suggests that even highly dispersive organisms like bryophytes are not equipped to fully track the rates of ongoing climate change in the course of the next decades.

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Despite a growing number of climate change mitigation policies, anthropogenic greenhouse gas emissions have continued to increase since the pre-industrial era. Globally, an average warming of 1.0 °C as compared to pre-industrial levels has been reported and is expected to reach 1.5 °C between 2030 and 2052, with substantial regional variations. In the Arctic for instance, two to three times higher warming rates than the global annual average are expected[1]. The impacts of this global warming on biodiversity have been largely documented[2] and climate change has been identified as one of the major biodiversity threats[3,4], with the worst-case scenarios leading to extinction rates that would qualify as the sixth mass extinction in the Earth history[5].

While climate change is making some current habitats unsuitable, it is also expected to create newly suitable areas for species to occupy. The extent to which species have the ability to balance the loss of suitable habitats by shifting their ranges and track areas of suitable climate has, however, been debated[6–8]. Despite reports that many species lag behind climate change[9], nearly as many studies of observed latitudinal changes fall above as below the observed[10]. For plants in particular, empirical evidence for lagged migration is far from clear-cut[11]. While the coincident increase of species richness with climate warming towards high elevations is suggestive of a rapid response of communities to climate change[12], considerable lags in the future response to climate warming have been predicted for Alpine plants[13]. Such lag has also been observed in the field: Rumpf et al.[14] recently reported that 38% of plant species they investigated were not able to colonize all the sites that became climatically suitable to them.

Assessing range shifts and extinction risks involves an assessment of (i) the change in climatically suitable habitats over time and (ii) the species ability to adapt or migrate to track areas of newly suitable climate[15]. In this context, spatially explicit climatic suitability and distribution models (also called species distribution models, or ecological niche models) have been the most widely used tool to assess the impact of projected climate change on future species distributions and biodiversity patterns[16]. Contrasting model predictions with actual distribution data revealed, however, that a substantial fraction of species are missing from areas projected as suitable[17,18]. This, together with the significant effect of geographic distance on the taxonomic and phylogenetic turn-over of species communities[17,19,20], points to the need to account for dispersal limitations when predicting species distributions under climate change[21,22]. Mounting evidence therefore suggests that approaches integrating mechanical dispersal processes into climatic suitability and distribution models have higher predictive accuracy in forecasting species range shifts than structurally simpler models that only account for species' correlates with climate[23,24].

The primary goal of the present study is to determine the extent to which highly efficient dispersers like bryophytes can mitigate the loss of suitable habitats through rapid colonization of newly suitable areas. The relevance of bryophytes, which represent the second most diversified group of land plants after the angiosperms[25], in range shift studies, is twofold. First, bryophytes hold exceptional importance in the control of global carbon fluxes and climate because of the vast stores of carbon bound-up in peat[26]. In particular, more carbon is stored in *Sphagnum* than in any other genus of plant[27]. Second, bryophytes lack roots and therefore cannot uptake water directly from the water table, making them reliant on atmospheric precipitations. Furthermore, bryophyte species of temperate biomes exhibit lower optima and tolerance to warm temperatures than their angiosperm counterparts[28] (but see ref. [29]). These specific ecophysiological features make bryophytes ideal indicators of the impact of climate change on biodiversity patterns.

Here, we implement a hybrid statistical-mechanistic approach that accounts for temporal and spatial variation of both climatic conditions and wind connectivity to predict potential shifts in distribution across Europe for 40 bryophyte species until 2050, at a spatial resolution of 1 km^2. We show that projected rates of range loss largely exceed the proportion of newly suitable habitats

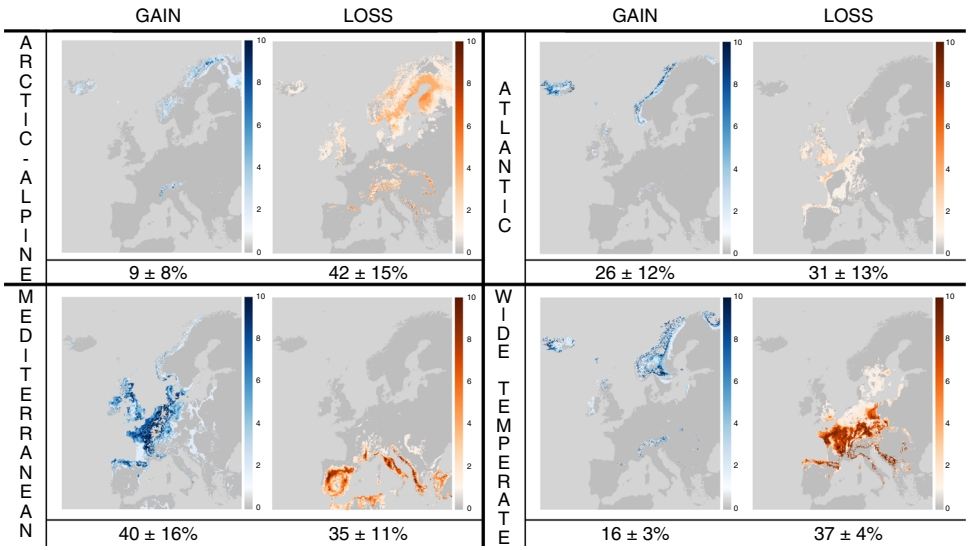

Fig. 1 Predicted impact of future climate change for the potential distribution of European bryophytes. The maps represent the distribution of 1 km^2 pixels predicted to become climatically suitable and unsuitable in 2050 for 10 representative bryophyte species of each of the four main biogeographic elements in Europe (Mediterranean, Atlantic, wide-temperate and Arctic-Alpine) using ensemble of climatic suitability models with the MPI-ESM-LR Global Circulation Model under scenario RCP8.5 (see Supplementary Fig. 1 for scenario RCP4.5 and Supplementary Figs. 2 and 3 for the two RCPs with the HadGem2-ES Global Circulation Model). Colours represent the proportion of species, computed over 10 species per biogeographical elements (individual maps are available from Figshare, DOI: 10.6084/m9.figshare.8289698), for which a pixel becomes suitable (blue) and unsuitable (red). Numbers indicate the average (±S.D.) percentage of the predicted increase (number of pixels that become suitable in 2050) and loss (number of pixels that become unsuitable in 2050), respectively, of suitable area in 2050 as compared to the extent number of suitable pixels.

that could effectively be colonized, suggesting that even highly dispersive organisms such as bryophytes might not be equipped to track the rates of ongoing climate change in the course of the next decades.

Results

We predicted range shifts under changing climate conditions until 2050 in 40 bryophyte species representative of the Mediterranean, Atlantic, wide-temperate and Arctic-Alpine biogeographic elements. The climatic suitability models exhibited high average True Skill Statistics (TSS) and Area Under The Curve (AUC) of a ROC plot (Receiver Operating Characteristics) statistics[30] of 0.78 ± 0.12 and 0.93 ± 0.05 respectively, when models were evaluated against test sets corresponding to 20% of the data (cross-validation). These models did not show any apparent signature of overfitting, as only a very slight increase in AUC and TSS (0.81 ± 0.13 and 0.94 ± 0.05, respectively) was observed when these statistics were computed at the level of the entire dataset (Supplementary Table 1).

With the MPI-ESM-LR Global Circulation Model (GCM), the highest relative rates of range loss are predicted for the Arctic-Alpine element, with an average loss of 40 ± 12% and 42 ± 14% and an average gain of 9 ± 7% and 9 ± 8% under the Representative Concentration Pathway (RCP) 4.5 and 8.5 climate change scenarios, respectively (Fig. 1, Supplementary Table 2 and Supplementary Fig. 1). The highest rates of relative range expansion are predicted for the Mediterranean element, with a 32 ± 10% (35 ± 10%) loss against a 38 ± 14% (39 ± 15%) gain, due to the clear tendency for a northern shift of the climatically suitable area (Fig. 1 and Supplementary Fig. 1). Similar, but even more dramatic predictions in terms of range loss, with a maximum of 73 ± 6% in the wide-temperate element, were obtained with the HadGem2-ES GCM (Supplementary Table 2 and Supplementary Figs. 2 and 3).

Simulated colonization rates (i.e., the ratio between the number of effective colonization events and the number of pixels becoming suitable by 2050) are displayed in Fig. 2 and Supplementary Fig. 4 (MPI-ESM-LR GCM under RCP scenarios 8.5 and 4.5, respectively) and Supplementary Figs. 5–6 (HadGem2-ES GCM under RCP scenarios 4.5 and 8.5, respectively).

There was a clear impact of release height on colonization rates, whose median ranged from 4% at 0.03 m to 63% at 10 m for the largest spores at maximum wind speed, and between 59% and 84% at 0.03 m for small and medium-sized spores, respectively, whatever the long-distance dispersal probability. At release heights of 1 and 10 m, colonization rates reached 98% and 99% for small and medium-sized spores, respectively (see Fig. 2 for scenario RCP8.5, with similar trends for scenario 4.5 in Supplementary Fig. 4 and for the HadGem2-ES GCM under RCP scenarios 4.5 and 8.5, Supplementary Figs. 5 and 6). Wind speed mostly played a role for the largest spores, whose colonization rates were 1–57 times higher when maximum vs average wind layers were employed, but its impact was lower for smaller spores. Finally, spore size also substantially impacted colonization rates, with a median <1 to 7% for large spores, 25 to almost 100% for medium-sized spores, and 61 to almost 100% for small spores depending on release height and long-distance dispersal probability under average wind conditions.

Running the simulations beyond 2050 to determine the time-lag of the colonization of newly suitable habitats, i.e., how many years would be needed for species to fully colonize all the climatically suitable habitats after 2050, we found, using release height values based on habitat preferences and maximum wind speed layers, that, on average, 80–100% and 25–70% of the species would need more than 500 years to successfully colonize all the newly suitable habitats when the long-distance dispersal probability was set to 0 and 0.1, respectively (Table 1 and Supplementary Table 1). Depending on climate change scenarios,

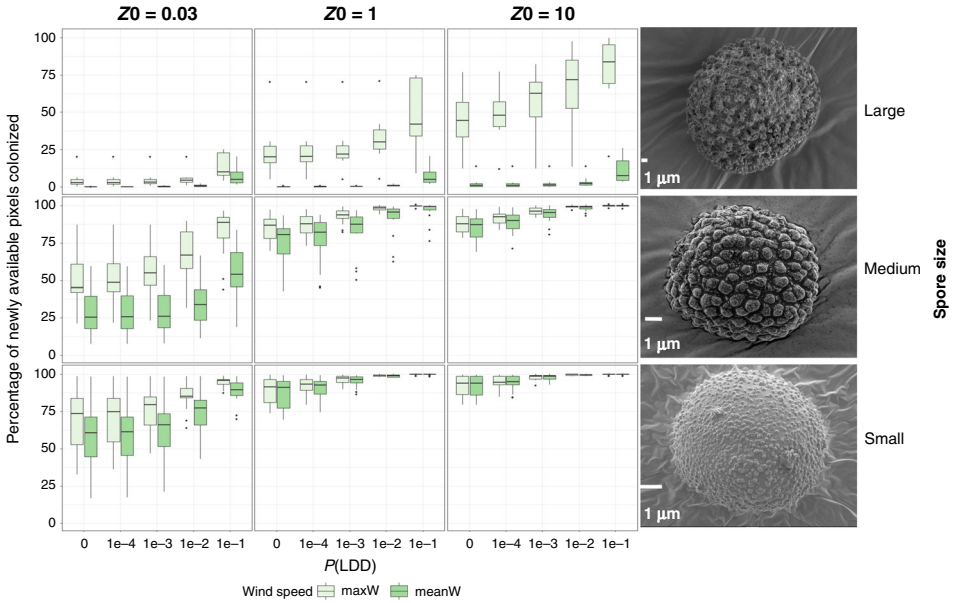

Fig. 2 Colonization rates of areas predicted to become climatically suitable due to climate change in European bryophytes. The box-plots (showing the 1st and 3rd quartiles (upper and lower bounds), 2nd quartile (centre), 1.5* interquartile range (whiskers) and minima-maxima beyond the whiskers) represent simulated colonization rates expressed as the ratio (*100), averaged over 30 replicates, between the number of effective colonization events (including effective colonization events that eventually got extinct at the end of the simulation) and the total number of pixels becoming suitable by 2050 in 40 selected bryophyte species in Europe as a function of spore size (a: <20 µm; b: 20–50 µm; c: >50 µm), release height Z0, wind speed, and probability of long-distance dispersal P(LDD), with the MPI-ESM-LR Global Circulation Model under climate change scenario RCP8.5 (see Supplementary Fig. 4 for scenario 4.5). The right panel illustrates selected SEM photographs of spores of *Scleropodium touretii* (small spores), *Ulota bruchii* (medium-sized spores) and *Archidium alternifolium* (large spores).

Table 1 Time-lag of the colonization of newly suitable habitats in 2050 for 40 selected bryophyte species in Europe, as assessed by MigClim dispersal simulations under changing climate conditions defined by the MPI-ESM-LR (MPI) and HadGem2-ES (HE) Global Circulation Models and climate change scenarios RCP4.5 and 8.5.

MPI4.5	MPI8.5	HE4.5	HE8.5
LDD = 0			
80%	98%	100%	98%
10%	0%	0%	2%
111 ± 126 years	149 years	-	-
LDD = 0.1			
70%	35%	25%	27%
22%	25%	25%	30%
21 ± 6 years	66 ± 85 years	86 ± 119 years	98 ± 141 years

LDD = 0 and 0.1 refer to the probability of long-distance dispersal implemented by the model, respectively. For each GCM, climate change scenario and LDD probability, we indicate (i) the percentage of species that failed to colonize all newly suitable habitats by 2050 after 500 years (top); (ii) the percentage of species that fully colonized all newly suitable habitats by 2050 and are hence at equilibrium with climate conditions (middle); and (iii) for the remaining species, the average (±SD) number of years required to fully colonize all newly suitable habitats after 2050 (bottom) (see Supplementary Table 2 for detailed information for each species).

only 0–10% and 22–30% of the species fully colonized all newly climatically suitable areas by 2050 when the long-distance dispersal probability was set to 0 and 0.1, respectively, and were hence at equilibrium with the environment (Table 1). The remaining species required, on average, 21 ± 6 years to 98 ± 141 years after 2050 before the colonization rate reached 100% of the newly suitable pixels depending on climate change scenarios and LDD probability (Table 1).

The ratio between the rates of range loss and gain at the end of the simulation in 2050 is displayed in Fig. 3, and evidences a clear pattern of substantial range contraction. Median ratios between predicted range loss vs expansion until 2050 across species ranged between 1.6 and 3.3 depending on climate change scenarios when only shifts in climatic suitability were considered, but between 34.7 and 96.8 depending on climate change scenarios and dispersal kernels when effective colonization was considered (Supplementary Table 2). With the global circulation model HadGem2-ES, the median loss/gain ratio was the highest in the case of the wide-temperate element (~75:1) as compared to a median ratio of slightly more than 50:1 for the other elements. With the MPI-ESM-LR Global Circulation Model, the median loss/gain ratio was the highest in the case of the Alpine-Artic element (~50:1) as compared to a median ratio of slightly more than 25:1 for the other elements.

Discussion

Simulating wind dispersal across a variable landscape is a challenging task because spatial variations in wind speed, topography and canopy structure affect the probabilities of colonization during the transportation and deposition phases[31]. Substantial variation in environmental heterogeneity affecting both climatic suitability and the ability of species to disperse therefore required developing a spatially explicit modeling framework. Previous studies that attempted at simulating wind dispersal under changing environmental conditions either (i) implemented constant dispersal kernels or randomly sampled prior distributions of migration rates at large scales[11,32,33], or (ii) used detailed models based on local wind conditions and accounting for population dynamics, but could only do so over a limited geographical extent[34,35]. In contrast, our approach allowed us to assess the impact of climate change on a group of wind-dispersed plants, bryophytes, by taking into account local variations in niche suitability and dispersal limitations at a continental scale.

Our simulations are, however, based on a number of simplifications due to limitations in the availability of empirical data. These limitations include, most importantly, the assumptions that dispersal is isotropic, that newly colonized cells are readily considered as sources, thereby ignoring demography, that there is no competition and that microclimatically suitable pixels can serve as migration sources. These assumptions result in an over- rather than an under-estimation of colonization rates, so that our approach is conservative in the sense that, as in Dullinger et al.[11], our results should be at the upper bound of those achievable. Despite this, only a portion of the areas projected to become climatically suitable are predicted to be effectively colonized by 2050. Median ratios between predicted range loss and expansion across species ranged between 1.6 and 3.3 depending on climate change scenarios when only shifts in climatic suitability were considered and increased to between 34.6 and 96.8 depending on dispersal kernels when effective colonization was considered. There was, however, substantial regional variation, as the Arctic-Alpine species pool was predicted to experience the highest range loss (39 ± 15%), whereas the wide-temperate species pool exhibited the lowest net decrease of 18 ± 4%, followed by the Mediterranean species pool with 24 ± 14%. While the Arctic-Alpine species pool was indeed identified as one of the most sensitive to climate warming, the results reported here for Mediterranean bryophytes sharply contrast with the alarming predicted range loss of 60% reported in angiosperms[36]. We suggest that this difference is due to the much wider distribution range, higher dispersal capacities and, potentially, broader climatic niche of Mediterranean bryophytes as compared to their angiosperm counterpart. This is best illustrated by the large differences in rates of local endemism between the two groups, as more than 60% of Mediterranean endemic angiosperm species are restricted to a single region[37] and are, hence, prone to extinction if they fail to colonize newly suitable areas, whereas there is no local endemism reported to date in the Mediterranean bryophyte flora[38].

While bryophytes successfully back-colonized areas of suitable climate since the end of the last glacial maximum, 18,000 years ago[39], our results suggest that, at best, ~30% of the species would be at equilibrium with their environment by 2050. This indicates that bryophytes are not equipped to track the very fast rates of ongoing climate change projected for the course of the next decades. Although recent evidence for synchronized increases in species richness towards high elevations and global warming points to rapid colonization potential of newly available habitats[12], our results, together with other analyses investigating species-specific responses[13,14,40], suggest that changes in diversity patterns tend to mask considerably the delays observed at the level of individual species. In fact, a growing body of evidence supports the idea that plant species spread rates are consistently expected to be much lower than the velocity of climate change[11,33–35]. This highlights the crucial role of integrating dispersal when attempting to predict future distribution ranges[22–24], even in apparently highly dispersive organisms like bryophytes.

Methods

The methodological framework for simulating the dispersal of bryophytes under changing climate conditions is presented in Fig. 4. A grid of pixel-specific environmental conditions and dispersal kernels, combining information on species dispersal traits, local wind conditions, as well as landscape features affecting dispersal by wind, is generated and used as input in simulations of species dispersal in the landscape under changing climate conditions.

Data sampling. The European bryophyte flora includes 1817 native or naturalized species[41]. Because information on bryophyte species distribution is scarce and very heterogeneous, challenging the application of climatic suitability models[42], we

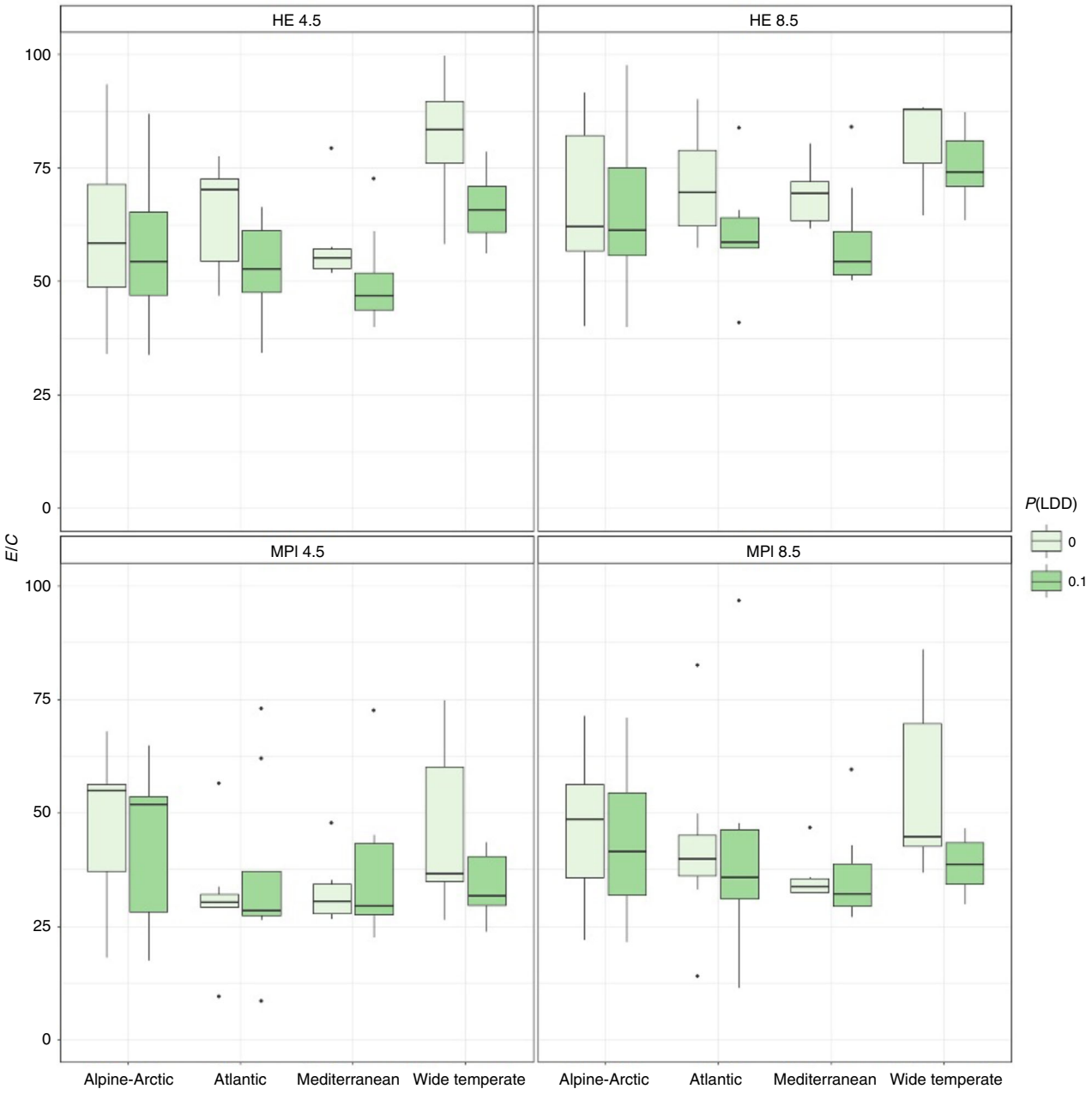

Fig. 3 Predicted rates of future extinction and colonization of areas becoming newly suitable due to climate change in European bryophytes. The boxplots (showing the 1st and 3rd quartiles (upper and lower bounds), 2nd quartile (centre), 1.5* interquartile range (whiskers) and minima-maxima beyond the whiskers) represent the ratio *E/C*, averaged over 30 MigClim replicates, between the predicted rate of range loss *E* (fraction of initially suitable cells that became unsuitable by 2050) and the rate of simulated effective colonization events *C* (fraction of newly suitable cells by 2050 that were effectively colonized) in 40 selected bryophyte species from the four main biogeographic elements in Europe. Results are shown for two selected dispersal kernels (release height set depending on species habitat preferences, maximum wind layer, and long-distance dispersal probability of 0 and 0.1), two global circulation models (MPI: MPI-ESM-LR and HE: HadGem2-ES) and two climatic scenarios (RCP4.5 and 8.5).

selected 10 species based upon their representativeness for each of the four main biogeographic elements (i.e., groups of species sharing similar distribution patterns), namely the Arctic-Alpine, Atlantic, Mediterranean, and wide-temperate elements (Supplementary Table 2). For each of these species, we downloaded data from the Global Biodiversity Information Facility (https://www.gbif.org). We excluded data collected before 1960, which represented, on average, 41 ± 12% of the data available, for two reasons. First, old records often lack sufficiently precise location information. Second, we wanted to avoid a potential mismatch between old observations and current climate conditions used for modeling. To complete these data and generate a dataset across the entire range of each species in Europe, we specifically performed a thorough literature review to document their occurrence from more than 600 sources. Only points that were separated by at least 0.1° from each other were subsequently retained for modeling ("ecospat.occ. desaggregation" function in Ecospat 3.1[43]) to avoid sampling bias and reduce the risk of spatial autocorrelation. Altogether, the number of observations available for each species ranged between 55 and 34,035 (database available from Figshare, https://doi.org/10.6084/m9.figshare.8289650).

Average spore diameter was recorded for each species from Zanatta et al.[44] and references therein. Species unknown to produce sporophytes were assigned a spore size of 150 µm to take dispersal through larger asexual propagules into account. Spore settling velocities V_t and release height (0.03, 1 and 10 m, which roughly correspond to habitat preferences for ground-dwelling, saxicolous, and epiphytic species, respectively) were determined for each species (Supplementary Table 2) following Zanatta et al.[44].

Nineteen bioclimatic variables, averaged over the period from 1970 to 2000, were retrieved from WorldClim 1.4 at a resolution of 30 arc-seconds[45]. Although

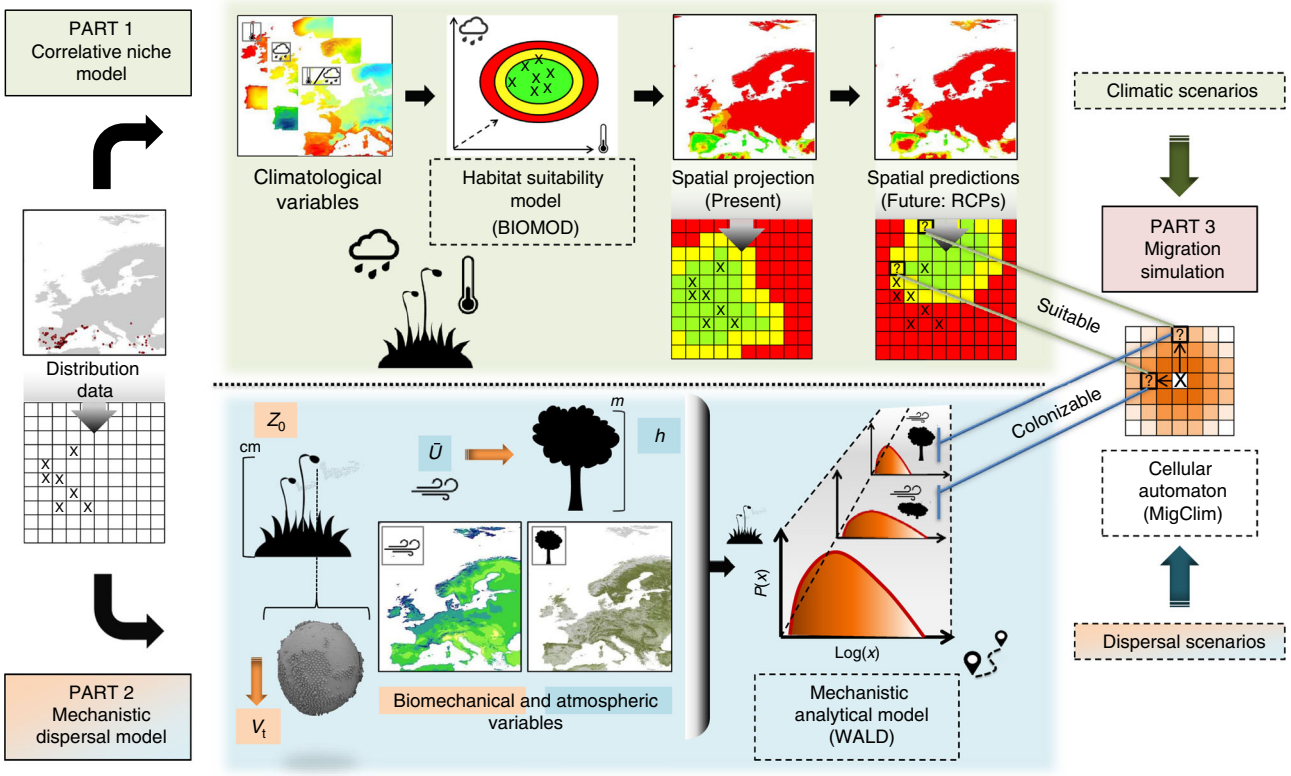

Fig. 4 Overview of workflow implemented in the present study to integrate mechanistic dispersal kernels and correlative climatic suitability models in simulations of future wind-dispersed species distributions under climate change. Species distribution data (left) are combined with climatic variables to produce climatic suitability models that are calibrated under present and projected under future climatic conditions (Part 1) and used to build mechanistic dispersal models (Part 2). The latter combine species intrinsic features (spore settling velocity V_t and release height Z_0) and extrinsic environmental features (mean horizontal wind speed $\bar{U}$ and canopy height h) to generate maps of spatially explicit dispersal kernels. Climatic suitability and dispersal kernel maps, updated at regular intervals, are finally combined to parameterize simulations of dynamic range shifts under changing climatic conditions (Part 3).

snow is an important driver of species distributions in Arctic regions[46], the lack of sufficiently detailed information on snow precipitation across Europe prevented us from implementing this variable.

Given the spatial grain of our study, the hypothesis that some species will persist in small microhabitats, where temperatures can be cooler and humidity higher than in the surrounding environment, cannot be rejected. Data at finer scales for both present and future conditions would therefore be desirable[47]. Recently developed methods to generate fine-grained climatic data taking into account microclimatic effects modulated by microtopographic variation in the terrain, vegetation cover and ground properties using energy balance equations cannot, however, yet be implemented across large spatial scales[48].

For future climate conditions, a wide range of GCMs have been described and their variation represents the largest source of uncertainty in future range prediction studies[49]. No criterion exists to evaluate GCMs, whose performance may vary among regions and variables[50]. Due to computational constrains associated with our migration simulations (see below), we followed Didersky et al.[51]. and selected two GCMs that reflected the highest and lowest levels of predicted changes due to climate change for two angiosperm species in Europe[50], namely MPI-ESM-LR[52] and HadGem2-ES[53]. For each GCM, we analyzed two climate change scenarios. These scenarios are expressed by the representative concentration pathways (RCPs), using values comparing the level of radiative forcing between the preindustrial era and 2100. The moderate scenario RCP4.5 assumes 650 ppm CO_2 and 1.0–2.6 °C increase by 2100, and refers to AR4 guideline scenario B1 of IPCC AR4 guidelines. The pessimistic scenario RCP8.5 assumes 1350 ppm CO_2 and 2.6–4.8 °C increase by 2100, and refers to A1F1 scenario of IPCC AR4 guidelines[54]. Climatic data for each GCM and each RCP were averaged for each of the four time periods considered, i.e., 2010–2020, 2020–2030, 2030–2040 and 2040–2050.

Monthly average and daily maximum wind speeds measured at 10 m as well as predicted wind speeds for the same ten-year time periods between 2010 and 2050, were computed from EURO-CORDEX (https://euro-cordex.net). Canopy height data were obtained from the global scale mapping of canopy height and biomass at a 1-km spatial resolution[55]. Wind speed and canopy height were sampled for each pixel and each time-slice to generate kernel maps through time (see below).

Deriving climatic suitability maps. The correlation among the 19 bioclimatic variables was computed from 50,000 random points. To avoid multicollinearity, five bioclimatic variables with a Pearson correlation value of $R < 0.7$ (as recommended in ref. [30]) were selected. These variables were: mean of monthly temperature range, temperature seasonality, mean temperature of warmest quarter, precipitation of wettest month and precipitation of warmest quarter. Since the geographic background should not only reflect the extant, but also the potentially occupied range in the past[56], and since, in bryophytes, models built from large geographic backgrounds are recommended[57], pseudo-absence points were sampled from a random selection from all points within the studied area excluding available presence points across Europe.

To account for model uncertainty, we generated ensemble models[58] using generalized linear model (GLM)[59] and boosted regression trees (GBM)[60] with the package biomod2 3.3–7[61]. Following Barbet-Massin et al.[62], 10,000 pseudo-absence points were sampled for GLM and then down-weighted to give them same overall prevalence as presences. For GBM, we sampled a number of pseudo-absence points identical to the number of datapoints. For GLM, the default parameter set (selection procedure via AIC, quadratic model, interaction level = 0, interaction level between variables considered, logit function) was used. For GBM, 5000 trees were included, the maximum depth of each tree was set to 5, the fraction of the training set observations randomly selected to propose the next tree in the expansion was set to 0.8. All other parameters were set to default (Bernouilli distribution, minimum number of observations in the terminal nodes of the trees = 5, shrinkage = 0.001, Number of cross-validation folds = 3). Ten replicates were run and, for each run, 80% of the data was used to calibrate the models, whereas the remaining 20% was kept aside to evaluate the performance of the model using the AUC and TSS metrics. We generated a consensus model of the 10 replicates for each of the GLM and GBM models, wherein each individual model contributed proportionally to its goodness-of-fit statistics. Finally, we computed the suitability at each pixel based on the average of the two GLM and GBM consensus models. Because, despite our thorough literature survey to document species distributions, the number of actually sampled points is a dramatic under-estimation of the actual number of occupied pixels by the species across the study area, all pixels identified as climatically suitable by binarized climatic suitability model projections were employed as initial distribution points for migrations during the first time slice.

This could lead to an overestimation of the number of source pixels and raises the issue that, like in any hybrid correlative-mechanistic model, datapoints are employed both for inferring the niche and initiating dispersal simulations, whereas datapoints are themselves the result of a dispersal process[63]. If, due to dispersal constraints, a species is absent from climatically suitable conditions, climatic suitability models may therefore underestimate species niche range[63]. Although bryophytes are extremely good dispersers, so that, unlike in some angiosperm species[18], there is no mismatch between the predicted and observed northern limit of distribution[39], the present analyses suggest that there is a time-lag of more than a century before newly suitable areas are fully colonized. Nevertheless, our datapoints were sampled across the entire European range of the species, encompassing the full range of climatic conditions that they can experience, so that the potential failure to incorporate localities where the species had not time to disperse yet would not affect the boundaries of our global niche estimate.

The ensemble model was then projected onto future climatic layers using two GCMs and two RCPs per GCM (see above). A key issue with modeling responses to climate change is that we do not fully understand how models made under current conditions will transfer to future conditions. Models developed using too many predictors may run the risk of overfitting to local conditions, restricting the predictive power of the model[64,65]. Tests of transferability across taxa and geographic locations have, however, failed to demonstrate consistent patterns, and a general approach to developing transferable models remains elusive[66]. Here, we compared the ROC and maxTSS values computed from the test sets (20% of the data) to those observed at the level of the entire dataset, assuming that these statistics at the level of the entire dataset would substantially drop at the level of the test sets in case of severe issues of overfitting.

The continuous suitability index was transformed into a binary presence/absence model, using maximum TSS to reclassify values.

Dispersal simulations under changing climate conditions

The MigClim model. Dispersal simulations under changing climate conditions were performed with a modified version of Migclim[67] adapted for wind dispersal. To simulate dispersal under climate change, MigClim requires information on species dispersal capacities, a map of species initial distribution, a map of present climate conditions, and maps of future climate conditions at p intervals that divide the period between time present and the end of the simulations, set by the user, into p climatic periods. In MigClim, source pixels are represented by actually occupied pixels and target pixels are pixels that newly become climatically suitable under climate change. Dispersal simulations are performed from source pixels into target pixels as follows (see Fig. 2 in Engler et al.[68]):

1. For each target pixels, all the potential source pixels located within a user-defined range are identified.
2. The probability that the target pixel is colonized from all the potential source pixels is computed through the probability *P*col (see below). Optionally, long-distance can be added to the simulation, with a user-defined range and probability.
3. These steps are repeated *n*Disp times, with *n*Disp typically set to 1 year, until the end of the first climatic period.
4. At the end of each of the p climatic periods, pixels that are no longer suitable due to changes in environmental conditions have their values reset to zero, and climatic suitability is updated to reflect environmental change, potentially resulting in a series of newly suitable target pixels.

To define *P*col, MigClim implements a dispersal kernel, which is a vector indicating the probability of dispersal $P(x)$ as a function of the distance from the source. Since dispersal from a source pixel could take place in any direction, MigClim implements a coefficient of diffusion called Surface_j, which corresponds to the number of pixels belonging to a same distance class from the source, to compute the probability that a diaspore from a source pixel ends-up in a target pixel and not in any other pixel located at the same distance range:

$$P\left(\text{pixel}_j\right) = \frac{P(x)}{\text{Surface}_j} \quad (1)$$

To account for the number of diaspores produced by a source pixel j, MigClim implements a parameter called Successful Seeds, which accounts for the number of seeds produced by a source pixel j and allows for turning individual dispersal event probabilities into species spread rates.

$$P_{\text{Disp}}(\text{pixel}_j) = 1 - \left(1 - P_{\text{Seed}}(\text{pixel}_j)\right)^{\text{SuccessfulSeed}} \quad (2)$$

Finally, $P(\text{pixel}_j)$ values are computed at increasing distances from the source and combined to generate a global probability of colonization *P*col from n potential source pixels:

$$P\text{col} = 1 - \prod_{i=1}^{n}\left(1 - P_{\text{disp}(i)} \times P_{\text{mat}(i)}\right) \quad (3)$$

where $P_{\text{mat}(i)}$ is a probability that is function of the time as the source pixel I became occupied and represents the increase in reproductive potential of source pixel i over time.

Implementing the Wald model in MigClim for simulating dispersal by wind. We developed a new version of Migclim, MigClim 1.7[69], designed for wind dispersal. While a single kernel was employed across the landscape until the end of the simulations in the previous implementation of MigClim, we employed a wind-dispersal kernel that was sampled for each pixel individually to account for variations in wind conditions and was modified at the same time as the p climatic change intervals to take future wind conditions into account.

We employed the Wald model[70] to infer dispersal kernels. The WALD model was initially developed[70] and largely used for wind-dispersed seeds[34,35], so that its use for smaller particles could be questioned. Bryophyte spore-trapping experiments in fact revealed that the tail of the dispersal kernel is, beyond hundreds of meters, not distance-dependent, suggesting that, once a spore is airborne, it could disperse over hundreds to thousands of kilometers, regardless of the distance from the source[71]. Spatial genetic structures consistently show, however, significant isolation-by-distance patterns for all distance classes, evidencing that realized colonization rates are distant-dependent[72] and justifying the implementation of a mechanistic model such as WALD. Furthermore, the WALD model assumes that (i) the slippage velocity between the particles and surrounding air is zero, leading to an infinite drag coefficient, so that the particles and surrounding air parcels are tightly coupled, and that (ii) the diaspore terminal velocity is reached instantly after release. These conditions are precisely met in small particles, which (i) are characterized by low Reynolds numbers, and hence, high drag coefficients, and (ii) almost readily reach terminal velocity after release. The WALD model has thus also been applied to small particles such as pollen grains and spores[73,74].

The Wald model[70] defines the probability $P(x)$ of colonization at distance x from the source depending on intrinsic (e.g., settling velocity, height of release) and extrinsic (e.g., wind speed) parameters, across the distance range between the source and target pixels, as follows:

$$P(x) = \sqrt{\frac{\lambda'}{2\pi x^3}}\exp\left(\frac{\lambda'(x-\mu')^2}{2\mu'^2 x}\right) \quad (4)$$

With $\mu' = \frac{H\bar{U}}{\text{Vt}}$, $\lambda' = \left(\frac{H}{\sigma}\right)^2$ and $\sigma^2 = 2Kh\frac{\sigma_w}{\bar{U}}$

where x is the distance from the source, $\bar{U}$ is the horizontal mean wind speed at the height of seed release, H is the release height, h accounts for canopy height, Vt is the diaspore terminal velocity, K is von Karman's constant (0.4), and σ_w is a turbulence parameter corresponding to the standard deviation of the vertical wind velocity.

Starting from the centroid of a source pixel, we finally integrate the Wald model over the shortest and largest distances between the source and target pixels to obtain the probability of colonization of the latter.

Parameter estimation. We derived the turbulence parameter σ_w from wind speed data and canopy height[55]. $\sigma_w = 1.25\,u^*$, where u^* is the wind-induced friction velocity depending on canopy height. Since wind speed is typically measured over short vegetation (h_s, set at 0.3 m), we first inferred σ_w above taller vegetation of variable height h from the wind-induced friction velocity measured above short vegetation, u_s^*. Hypothesizing that, at the top of the atmospheric surface layer (~200 m), the mean velocity is not affected by the texture of the ground vegetation,

$$u^* = u_s^*\left(\log(200) - \log\left(\frac{h_s}{10}\right)\Big/\left(\log(200) - \log\left(\frac{h}{10}\right)\right)\right) \quad (5)$$

Following Nathan et al.[35], u_s^* was estimated using von Karman's formula from the measured wind speed $\bar{U}_s$:

$$\bar{U}_s = \frac{u_s^*\log\left(\frac{w}{Z0_s}\right)}{K} \quad (6)$$

where K is von Karman's constant (0.4), w is the height, at which the wind was measured (here 10 m), and $Z0_s = 0.1\ h_s$.

The friction velocity u^* for taller vegetation of height h was then derived using Eq. (5).

To derive the mean wind speed at the height of release H, we implemented either the logarithmic or exponential wind profile[75]. When the height of release H is roughly higher than the canopy height h, the logarithmic wind profile describes the decline in horizontal wind speed with decreasing height above the surface, due to the surface resistance, as:

$$\bar{U}_H = \frac{u^*\ln\left(\frac{H-d}{Z0}\right)}{K} \quad (7)$$

with $Z0 = 0.1$ h and $d = 0.7$ h.

In contrast, when the height of release H is below the canopy, we implemented the exponential wind profile:

$$\bar{U}_H = \bar{U}_h\exp\left(\alpha\left(\frac{H}{h} - 1\right)\right) \quad (8)$$

with the mean wind speed at canopy height $\overline{U_h}$ derived from Eq. (6), and α derived from Gualtieri and Secci[76] as $\alpha = 0.24 + 0.096Z_0 + 0.016\log^2 Z_0$, where $Z_0 = 0.1$ h

The parameters $\bar{U}$, h and σ_w are sampled for each pixel and each time-slice (10 years intervals) to generate kernel maps through time.

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We determined "Successful Seed" empirically following the calibration method of Engler and Guisan[67]. Although "Successful Seed" was determined once on the basis of a single empirical study[71] and kept constant across species, this study reported observed colonization rates at distances of hundreds of meters from the source colony, giving us a unique opportunity to make the link between our deterministic models and actual observations, increasing the realism of our approach. P_{mat} was set to 1.

Finally, in addition to short-distance dispersal events with a probability defined by the kernel described above, any pixel located at >10 km from a potential source could be colonized by LDD. The maximum LDD distance was set to unlimited based on phylogeographic evidence[39]. Following Robledo-Arnuncio et al.[31], we employed the results of previous Approximate Bayesian Computation methods for LDD inference from genetic structure data in bryophytes[39,77] to define the range of LDD probability values, set to 0, 10^{-4}, 10^{-3}, 10^{-2} and 10^{-1}.

Migclim simulations. We modeled the dispersal of a species under a climate change scenario over a period of 40 years, from 2010 to 2050. Starting with an initial distribution for the year 2010, the climatic suitability of cells was updated every 10 years to reflect the projected changes in climatic conditions under the considered climate change scenario. Since our simulations run over 40 years, we need four different climatic suitability maps. The wind layers were updated at the same 10 years intervals as the climatic data to produce series of spatially and temporally explicit kernel maps. We assume that our species disperse once a year, and hence, our simulations performed a total of 40 dispersal steps between 2010 and 2050. For each 10 years climatic period, pixels were identified as potentially suitable based on the binarized climatic suitability model projections. While climatic suitability thus drove colonization probability, a recent study raised the intriguing idea that spread rates at the migration front increase as climatic suitability decreases as a response to the need to seek for more suitable habitats[78]. In bryophytes, however, such a mechanism would be unlikely as inadequate resources and investment in environmental stress defence typically result in shifts from sexual to asexual reproduction[79].

For each species, we ran a sensitivity analysis by testing the impact of variation of the free parameters described above: two values of horizontal windspeed $\bar{U}$ (monthly average and daily maximum), three values of spore release height Z_0 (0.03, 1 and 10 m), and four values of LDD probabilities (see above). For each parameter combination, 30 MigClim replicates were performed.

We computed the ratio between the predicted loss of suitable area (fraction of initially suitable cells that became unsuitable by 2050) and the simulated effective colonization rate (fraction of newly suitable cells by 2050 that were effectively colonized) using two extreme values of the LDD probability range, that is, 0 and 0.1.

To determine the time-lag of the colonization of newly suitable habitats, the analyses were run for 500 years, keeping the environmental parameters at their 2050 values.

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

Occurrence data are available from Figshare (https://doi.org/10.6084/m9.figshare.8289650).

Code availability

Migclim 1.7 and all the R scripts for the analyses presented here are available on GitHub[69].

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Author contributions

A.G., A.V., F.Z. and R.E. designed the framework of the study. A.V., B.P., J.M. and R.G.M. collected the data. D.B., F.C., F.Z., O.B. and R.E. performed the analyses. A.V., F.C. and F.Z. wrote the paper with the assistance from all co-authors.

Competing interests

The authors declare no competing interests.

Additional information

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5. General discussion

Species distribution models are powerful tools to predict species range shift. However, these models rely on several assumptions (Guisan et al., 2017; Zurell et al., 2020a). In this thesis, I tested these assumptions in bryophytes, which are ideal models to study the impact of climate change on biodiversity patterns (He et al., 2016) and implemented a newly designed model of dispersal by wind in the context of climate change.

5.1. At which taxonomic level should SDMs be implemented?

The role of local adaptation in species diversification has been increasingly acknowledged (Chardon et al., 2020; Peterson et al., 2019; Sork, 2017), with major consequences for our ability to accurately infer species niches and, in particular, predict future distributions in the context of climate change (Hällfors et al., 2016; Maguire et al., 2018; Peterson et al., 2019; Valladares et al., 2014; Yannic et al., 2014). To address this issue, we compared the outcome of models built at the species and intraspecific level. Working on intraspecific lineages implies, however, that enough distribution data for genetically-identified specimens are available. In our study, the available number of occurrences in chapter I was small, from 12 to 93, raising concerns about model calibration and evaluation (Guisan et al., 2007; Liu et al., 2019; Proosdij et al., 2016; Støa et al., 2019; Wisz et al., 2008). We therefore used ensemble of small models, which have been developed for model calibration with small datasets (ESMs; Breiner et al., 2018, 2015; Lomba et al., 2010). For model evaluation, however, a minimum of 10 occurrences and 10 true absences is recommended (Jiménez-Valverde, 2020). The evaluation methodology recommended by Breiner et al. (2015,2018), i.e., computing and averaging metrics from the hold-out data across replicates, can nevertheless result in very small sample sizes for the evaluation data set. This is why we suggest here to evaluate ESMs by pooling the suitability values of the holdout data across replicates, this way assembling a larger evaluation set. As the same presence point is likely to be sampled in multiple replicates, the suitability values for each presence point can be averaged across replicates to avoid pseudo-replication, generating a series of suitability values independent from the data used to calibrate the models. These suitability values can then be combined with the pseudo-absence points to assess model performance. As a result, model performance is computed from roughly the total number of occurrence data available instead of averaging AUC, maxTSS and Boyce index computed from very small subsets of holdout data. Despite relatively high values of AUC, maxTSS and Boyce index, 2 of the 32 ESMs did, however, not exhibit significantly higher AUC and maxTSS values than those that would be expected by chance from null models, as proposed by van Proosdij et al. (2016). The evaluation procedure based on the construction of null models calibrated from pseudo-absences thus appears as a useful tool to discard unreliable models based on very small sample sizes, and we therefore strongly recommend its implementation for ESM (or even SDM) evaluation in general.

Distinguishing intraspecific differentiation when modelling species distributions had substantial consequences, as the combined projection of subclade models onto past, present and future climatic layers consistently predicted larger ranges than those resulting from clade models. Our results thus support the idea that lumping and splitting produce very different niche and distribution estimates (Hällfors et al., 2016). In contrast with the present results, Maguire et al. (2018), Moto-Vargas and Rojas-Soto (2016) and Cacciapaglia and Woesik (2018) reported that clade models tend to predict larger areas of suitable conditions than combined subclade models. Maguire et al. (2018) suggested that clade models may smooth across the climate–distribution relationships that are identified by subclade models, capturing a broader

niche representing more potential combinations of climate conditions. Alternatively, we suggest that this result may also arise from overfitting at the level of the subclade models, which are based on lower number of occurrence data than clade models. In turn, and in line with the present results, Pearman et al. (2010), Oney et al. (2013) and Valladares et al. (2014) reported that combined subclade models tend to predict larger areas of suitable conditions than clade models because subclade models can predict suitable areas that are geographically peripheral to areas predicted suitable by clade models (Pearman et al., 2010).

The substantial differences between the projections of clade and subclade models raise the question of the level at which modelling should be performed. To address this question, two criteria have been proposed based on model accuracy and analyses of niche overlap (Smith et al., 2019). AUC and MaxTSS are dependent on prevalence, and hence, not comparable among models based on different sampling sizes (Somodi et al., 2017). As Smith et al. (2019) emphasized, it is therefore challenging to compare clade and subclade models on an equal basis because of factors that are difficult to control, including range size and geographic extent, sample size and autocorrelation between training and test sets that varies in strength depending on whether occurrences are combined or divided.

The second criterion that could be employed to help deciding whether clade or subclade models should be applied is based on niche overlap analyses and niche similarity tests (Broennimann et al., 2012; Warren et al., 2008). In chapter I, niche conservatism was evidenced in half of studied species, but no sign of niche divergence was detected. In such conditions, and given the problems of model calibration and evaluation for small datasets, even when applying specifically designed techniques such as ESMs, we recommend to lump intraspecific lineages into a single clade model, allowing to generate a sufficient occurrence database at the species level (Hällfors et al., 2016). Using simulated data allowing an assessment of competing model performance, Qiao et al. (2017) in fact showed that, in the case of groups of rare, sister species, the projection of models built at the level of the pooled distributions of sister species (clade models) better match the known distribution of individual species (subclade models) when sister species share similar niches. Smith et al. (2019) argued against the use of niche similarity tests to decide whether fitting models at the levels of clade or subclade because two lineages shown to be more similar than expected by chance may still sufficiently differ in their environmental tolerances, so that their niches would be best modelled by splitting. In fact, the four species for which a signature of conservatism was found were not systematically the ones for which the mismatch between clade and subclade models was the lowest. While we certainly agree with Smith et al. (2019) that evidence for (or lack of) selectively based niche differentiation should ideally be based upon progeny tests and common garden experiments or association mapping of alleles with observed phenotypic differences across populations, such evidence is almost completely lacking in non-model organisms like mosses, wherein reduced morphologies further hamper the possibility to use aspects of life history or functional traits expected to experience strong selection.

In conclusion, we suggest that niche description and an assessment of niche overlap using the I and D metrics represent a useful contribution in the context of an increasing interest for integrative taxonomic approaches (Raxworthy et al., 2007), especially in small-sized organisms with reduced morphology such as bryophytes (see Vigalondo et al., 2019, and references therein). Given the genetic forces underlying the speciation process, it is, in fact, not appropriate to use morphological features as the sole criterion for species recognition (Egge and Simons, 2006). In chapter I, where lack of significant niche divergence among lineages is coupled with the absence of any morphological divergence between them, lineages may not

deserve recognition at the species level, although their genetic distinctiveness and mostly allopatric ranges suggest that they may be recognized as different units for conservation (Hedenäs, 2020, 2018, 2017, 2016).

Marcer et al., 2016 recommended that such intraspecific genetic differentiation should guide the design of SDMs studies. We suggest, however, that, in the absence of solid evidence for niche divergence among molecularly defined lineages, SDMs should be based on all available occurrence records at the level of species, ideally redefined based on molecular data or, in the absence of the latter, based on morphological species concepts. This will help generating datasets of sufficiently large size for modelling in organisms whose distributions are typically poorly documented, as in the case of complexes of rare species (Qiao et al., 2017).

A broad acceptance of the niche conservatism hypothesis, and whether niche conservatism persists across phylogenetic scales (Peterson, 2011), remains, however, to be demonstrated. We address these two issues hereafter.

5.2. Species distribution models and the phylogenetic niche conservatism hypothesis at different phylogenetic depth

To address the question of climatic niche conservatism at a broad taxonomic scale and its evolutionary 'lability', we analyzed in Chapter II the relationship between phylogenetic turnover and environmental drivers at different phylogenetic levels within an entire phylum of land plants, the Marchantiophyta or liverworts, which include about 7,500 species (Söderström et al., 2016). We generated π_{st}-through-time profiles, analogous to the β-diversity through time framework (Groussin et al., 2017), at 1 myr intervals along the phylogenetic time-scale. In fact, while environmental filtering may have left an imprint on patterns of taxonomic and phylogenetic turnover, pointing to climatic niche conservatism, its effect may, however, be perceived only at certain depths along the phylogenetic time-scale (Duarte et al., 2014; Mazel et al., 2017). For example, two areas may not share any species, but if their species all belong to the same higher taxonomic units due to strong phylogenetic niche conservatism, then the phylogenetic turnover between these two regions will be 0 at that taxonomic level. The phylogenetic scale used to define the structure of ecological assemblages may therefore also influence the relationships between phylogenetic patterns and environmental gradients depending on the degree of phylogenetic niche conservatism (Ndiribe et al., 2013; Wiens and Graham, 2005).

We showed that phylogenetic turnover of liverwort communities is significantly correlated with macroclimatic conditions, independently from geographic distance, adding to emerging evidence for the role of environmental filtering upon community assembly through time (Ndiribe et al., 2013; Pelissier et al., 2013a,b,c; Saladin et al., 2019; Segovia et al., 2020). The correlation between phylogenetic turnover and macroclimatic variation evidences macroclimatic niche conservatism at a world scale, reinforcing the idea that biome conservatism is a primary driver of present-day distribution patterns of biodiversity (Crisp et al., 2009; Segovia et al., 2020). Although evidence for niche conservatism is mounting in bryophytes (Johnson et al., 2015; Piatkowski and Shaw, 2019), we demonstrate here for the first time its relevance for shaping large-scale patterns of liverwort assemblage distributions.

The explanatory power of contemporary macroclimatic variation on phylogenetic turnover remained fairly constant towards deep branches and becomes insignificant only beyond 100 myrs, pointing to the crucial role of climatic niche conservatism for the assembly of liverwort assemblages over very large evolutionary time scales. The sharp decrease of the correlation between macroclimatic variation and phylogenetic turnover 100 myrs can be interpreted in terms of a burst of diversification (Laenen et al., 2014), especially obvious at the level of epiphytic lineages (Feldberg et al., 2014), triggered by the development of large, humid megathermal angiosperm forests, after which lineage diversification would have been constrained macroclimatically.

Our results have several consequences, for instance in terms of the application of such a pervasive biodiversity pattern as the increase of species richness towards the tropics, even in organisms with high dispersal capacities such as bryophytes. Most importantly, and regarding the underlying assumptions made while interpreting SDM projections into different geographic areas or temporal scales, evidence for macroclimatic niche conservatism at shallow phylogenetic depths and its long-term evolutionary persistence in liverworts supports the idea that the projection of the climatic niche onto future climatic layers is a realistic approximation of future species potential distributions.

5.3. Modelling range shift of wind-dispersed species under climate change

SDMs have been the most widely used tool to assess the impact of projected climate change on future species distributions and biodiversity patterns (Araújo et al., 2019; Guisan et al., 2017). Contrasting model predictions with actual distribution data revealed, however, that a substantial fraction of species are missing from areas projected as suitable (Keil et al., 2012; Svenning et al., 2008b). This, together with the significant effect of geographic distance on the taxonomic and phylogenetic turn-over of species communities (Keil et al., 2012; Saladin et al., 2019; Schurr et al., 2012), points to the need to account for dispersal limitations when predicting species distributions under climate change (Dullinger et al., 2012; Engler et al., 2009; Travis et al., 2013). Mounting evidence therefore suggests that approaches integrating mechanical dispersal processes into climatic suitability and distribution models have higher predictive accuracy in forecasting species range shifts than structurally simpler models that only account for species' correlates with climate (Fordham et al., 2018; Zurell et al., 2016).

In the context of a growing interest for predicting species range shift dynamics as a response to climate change, we presented in chapter III an integrative, spatially explicit method combining species distribution models and dispersal simulations specifically tailored for wind-dispersed organisms. We built on MigClim (Engler et al., 2012; Engler and Guisan, 2009), a framework initially simulating species movements in a heterogeneous environment through time, to propose a spatially explicit model tailored for wind-dispersed diaspores that accounts for variations in wind intensity across the landscape, topographic features affecting dispersal, and intrinsic species dispersal traits. A Wald analytical long-distance dispersal (WALD) model (Katul et al., 2005), which has been specifically developed for wind-dispersed plants (Bullock et al., 2012; Nathan et al., 2011), was used to generate a grid of spatially explicit dispersal kernels, combining information on species dispersal traits, local wind conditions, as well as landscape features affecting dispersal by wind. This kernel grid was then employed to inform MigClim's cellular automaton (Engler et al.,

2012; Engler and Guisan, 2009) to simulate species dispersal in the landscape under changing climate conditions.

The complementary of the present approach with previous studies implementing highly parameterized models taking, for instance, population growth rate, fine-scale wind information, variations in CO_2 concentrations and their impact on seed maturation at local scales of a few kilometers into account (Bullock et al., 2012; Nathan et al., 2011) comes from the fact that (i) spatio-temporal variation in climatic conditions, and whether species can cope with future climatic conditions, is explicitly taken into account and (ii) the large scale of the present study requires a spatially explicit model, which is newly developed, and captures a significantly higher variation and significantly higher colonization rates than when a non-spatially explicit approach is implemented.

Our approach is based on the implementation of the WALD model, initially developed (Katul et al., 2005) and largely used for wind-dispersed seeds (Bullock et al., 2012; Nathan et al., 2011), so that its use for smaller particles could be questioned. Bryophyte spore-trapping experiments in fact revealed that the tail of the dispersal kernel is, beyond hundreds of meters, not distance-dependent, suggesting that, once a spore is airborne, it could disperse over hundreds to thousands of kilometers, regardless of the distance from the source (Lönnell et al., 2012). A recent meta-analysis of spatial genetic structures consistently showed, however, significant isolation-by-distance patterns, evidencing that realized colonization rates are distant-dependent (Vanderpoorten et al., 2019), justifying the implementation of a mechanistic model such as WALD. Furthermore, the WALD model assumes that (i) the slippage velocity between the particles and surrounding air is zero, leading to an infinite drag coefficient, so that the particles and surrounding air parcels are tightly coupled, and that (ii) the diaspore terminal velocity is reached instantly after release. These conditions are precisely met in small particles, which (i) are characterized by low Reynolds numbers, and hence, high drag coefficients, and (ii) almost readily reach terminal velocity after release. The WALD model has thus also been applied to small particles such as pollen grains and spores (Rieux et al., 2014; Wang and Lu, 2017).

Variation in predicted colonization success was substantially impacted by release height. In bryophytes, release height is the most limiting factor due to their extremely small size. A seta typically measures a few cm at most and is inserted on a gametophyte that is also a few cm tall, so that the capsule lays at about 0.03 m above ground, leading to the smallest values of colonization probabilities observed. There is therefore a strong pressure for elevating the sporophyte above ground, either increasing gametophyte size and seta length, which is also important for maximizing the vibrations at the level of the capsule and maximize spore release (Johansson et al., 2014), or occupying elevated habitats such as rocks and trees, to maximize dispersal. This is consistent with the significant negative correlation between seta length and spore size observed across mosses, pointing to selection for increased dispersability (Crawford et al., 2009), and with the tendency of epiphytic species to display shorter setae than ground species (Hedenäs, 2001), wherein a long seta is advantageous to maximize spore dispersal above the herb layer.

Our approach allowed us to assess for the first time the impact of climate change in plants, taking into account dispersal limitations, at a continental scale. Median ratios between predicted range loss and expansion across species ranged between 1.6 and 3.3 depending on climate change scenarios when only shifts in climatic suitability were considered and raised to between 34.6 and 96.8 depending on dispersal kernels when effective colonization was considered. There were, however, substantial regional variations.

Indeed, Arctic-Alpine species were estimated to undergo the highest range loss (39 ± 15%), whereas the wide-temperate species bore the lowest decrease of 18 ± 4%, followed by the Mediterranean species with 24 ± 14%. The results for Mediterranean bryophytes strongly depart from the alarming predicted range loss of 60% in angiosperms (Thuiller et al., 2005). We suggest that this difference results from the much wider distribution range, greater dispersal capacities and, possibly, broader climatic niche of Mediterranean bryophytes than angiosperms. In fact, more than 60% of Mediterranean endemic angiosperm species are restrained to a unique region (Thompson, 2005) and are likely to become extinct if they fail to colonize newly suitable areas, whereas no endemic Mediterranean bryophyte species has been described to date (Patiño and Vanderpoorten, 2018).

While bryophytes successfully back-colonized areas of suitable climate since the end of the last glacial maximum, 18,000 years ago (Ledent et al., 2019), our results suggest that, at best, ~30% of the species would be at equilibrium with their environment by 2050. This indicates that bryophytes are not equipped to track the very fast rates of ongoing climate change projected for the course of the next decades. Although recent evidence for synchronized increases in species richness towards high elevations and global warming points to rapid colonization potential of newly available habitats (Steinbauer et al., 2018), our results, together with other analyses investigating species-specific responses (Dullinger et al., 2012; Engler et al., 2009; Ofori et al., 2017; Rumpf et al., 2019), suggest that changes in diversity patterns tend to mask considerably the delays observed at the level of individual species. In fact, a growing body of evidence supports the idea that plant species spread rates are consistently expected to be much lower than the velocity of climate change (Bullock et al., 2012; Dullinger et al., 2015; Nathan et al., 2011; Prasad et al., 2013). This highlights the crucial role of integrating dispersal when attempting to predict future distribution ranges (Briscoe et al., 2019; Cotto et al., 2017; Fordham et al., 2018; Travis et al., 2013; Zurell et al., 2016) , even in apparently highly dispersive organisms like bryophytes.

6. Conclusion and perspectives

We developed a new framework accounting for dispersal capacities for wind-dispersed organisms under climate change. We also showed the importance to include dispersal limitations for assessing range shifts under changing climate conditions, even in a very efficient dispersive taxon such as bryophytes, indicating that they are not equipped to track the very fast rates of the ongoing climate change. In addition, we evidenced that the niche conservatism hypothesis, which is a primary assumption when attempting at projecting species niches in space and time, is met in bryophytes from the infraspecific level to higher-order taxa, supporting the predictions derived from species distribution models under climate change.

The approach developed in the present thesis is, however, based on several assumptions, which call for future improvements. First, variation in population growth and reproductive biology in response to climate change should be taken into account. In angiosperms for instance, the increase in CO_2 concentrations affects seed maturation (Nathan et al., 2011). In bryophytes, mounting evidence points to increased frequencies of sex expression (Brinda et al., 2011) and fertility (Blackstock, 2018) as a response to increasing CO_2 concentrations and temperatures, but more data are needed to determine how this will translate in terms of an actual increase of spore production. Second, newly colonized cells are immediately considered as sources, thereby ignoring demography and assuming that there is no competition. Although maturation time can already be accounted for in hybrid SDMs (Engler & Guisan 2009, Dullinger et al. 2012), future modelling developments could consider incorporating effect of changed competition and other biotic interactions (Wisz et al. 2013). Third, wind dispersal is anisotropic and its intensity varies through time (Muñoz et al., 2004; Robledo-Arnuncio et al., 2014). Ideally, distributions of wind velocities and directions should be sampled. In practice, however, such an implementation is limited by the availability of high-resolution current and future wind data at the continental scale. Fourth, obtaining reliable estimates of dispersal has been a long-lasting challenge. In the present thesis, we employed mechanistic models that, however, included several parameters, and in particular, the proportion of effective migrants, that are difficult to assess. We discuss below potential strategies to address these shortcomings.

6.1. Including realized colonization rates into a dispersal simulator

As shown in this thesis, including dispersal capacities into species distribution models is important to give more precise predictions for the future, which is especially important notably for conservation plans (Serra-Diaz and Franklin, 2019; Urban et al., 2016; Zurell et al., 2016). Dispersal capacities can be assessed via direct and indirect approaches (Koenig et al., 1996). Direct approaches result from trapping experiments where dispersal kernels can be described and afterwards extrapolated beyond measurement scale (Clark et al., 2001). In plants, an efficient approximation of the potential dispersal capacity of a particle (e.g. spores or seeds) as the one presented in chapter III can be achieved via a combination of physical characteristics of the environment (e.g. canopy height, wind speed, turbulence, etc.) with species bio-mechanical characteristics such as settling velocities (Katul et al., 2005). In contrast, indirect approaches generally depend on analyzing spatial genetic structures. These two types of methods generate disparate estimates of migration rates, partly because direct approaches perform on areas that are spatially restricted and ignore the contribution of long-distance dispersal (Koenig et al., 1996; Thompson and Goodman, 1997). While direct techniques approximate migration rates and therefore do not take diverse parameters such as habitat

suitability and biotic interactions into account, indirect methods derive realized colonization rates (Vanderpoorten et al., 2019).

To derive dispersal estimates from genetic structure data under realistic demographic assumptions, new opportunities have emerged thanks to methodological improvements (Quinzin et al., 2017; Ray and Excoffier, 2009; Robledo-Arnuncio et al., 2014). Nonetheless, testing evolutionary hypotheses and assessing model parameters such as migration rates remains challenging (Kastally, 2018). In this context, spatially explicit coalescence models offer exciting opportunities to estimate migration and gene movements while trying to link the change of species extent and genetic-pattern fluctuations over time. These models thus allow to test alternative hypotheses in relationship with species geographic distributions (Excoffier and Heckel, 2006; Hoban et al., 2012, 2019). While classic coalescent models assume panmixia among individuals of pre-defined populations, spatially explicit coalescence models make no such assumption and instead, simulate the dispersal of each individual in the landscape (Kastally, 2018). As a result, these models can deal with patterns of isolation by distance (Dellicour et al., 2017, 2015, 2014b, 2014a; Joseph et al., 2016) and thus enable to infer realized colonization rates, which can afterwards be applied in dispersal simulators such as MigClim (Engler et al., 2012; Engler and Guisan, 2009) in order to predict the accessible future suitable areas for a species in the context of climate change (Engler et al., 2009).

6.2. Species distribution models, biotic interactions and bryophytes

A main issue of species distribution models is that they do not take biotic interactions such as competition, facilitation and parasitism into account (Guisan et al., 2017; Guisan and Rahbek, 2011; Wisz et al., 2013; Zurell et al., 2020a, 2020b). However, biotic interactions play an important role in species assemblages (Araújo and Luoto, 2007; Boulangeat et al., 2012; Bueno de Mesquita et al., 2016; Gutiérrez-Girón and Gavilán, 2010; Le Roux et al., 2012; Mod et al., 2016a, 2016b, 2015; Wisz et al., 2013) (Fig. 5), and this is increasingly true as the studied spatial scale decreases (Araújo and Rozenfeld, 2014; Mod et al., 2016c). Although biotic interactions are widely present in nature, it is challenging to measure them.

Originally, biotic interactions were experimentally characterized. One of the first methods was developed by Gause (1934) to evidence competitive exclusion and is still analogically used nowadays (Altermatt et al., 2015; Carrara et al., 2014; Giometto et al., 2014; Momeni et al., 2013). Biotic interaction experiments are usually based on comparisons of species fitness such as growth rates, biomass measured after addition a removal of one or several species (Ellenberg, 1953; Gause, 1934; Laska and Wootton, 1998) (e.g. Carlyle et al., 2010; Ingerpuu et al., 2005; Liancourt et al., 2005; Perkins et al., 2007; Qi et al., 2018; Švamberková et al., 2017). These techniques are strongly dependent upon the timing and modalities of the experiments (Laska and Wootton, 1998). In addition, they require an increasing amount of resources as the number of species raises, exponentially raising the number of experimental units (Udd et al., 2016).

In parallel to experimentation, statistical methods have been developed to characterize and quantify biotic interactions. These methods, usually requiring presence-absence data, allow to infer demographic relationships (Alroy, 2015; Forbes, 1907). One of the most recent approaches is based on null models (Blois et al., 2014; Gotelli and Ulrich, 2012) and uses SDM to infer species climatic niches (D'Amen et al., 2017; Scherrer et al., 2019). This method transforms a presence/absence matrix into a species co-occurrence

matrix, representing the associative force between each pair of species. It then applies two different null models: (1) non-constrained null models, allowing to infer the importance of randomness in species assemblages and (2) environmentally-constrained null models using probabilities from SDMs and enabling to estimate the importance of niche preferences. It afterwards analyses the spatial configuration in order to assess the importance of dispersal limitations for explaining non-coincidences. Finally, non-random species pairs that cannot be interpreted in terms of niche preferences nor non-overlapping distribution ranges are interpreted in terms of biotic interactions (D'Amen et al., 2017).

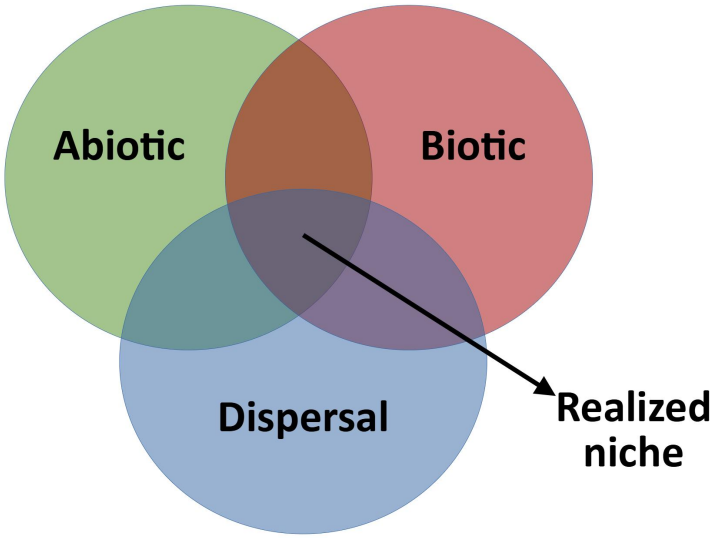

Fig. 5: The three main drivers of observed species ranges (redrawn from Poggiato et al., 2021; Soberón, 2007). Green and red disks represent the abiotic and biotic areas that are compatible with the species presence, respectively, while blue disks represent the area that the species can reach. The intersection of these three factors represents the space that the species can actually colonize, i.e., its realized niche.

Biotic interactions have been seldom investigated in bryophytes. As they are considered as pioneers, bryophytes rarely form saturated communities. This is why competition between bryophytes is controversial (Bergamini et al., 2001; Frego and Carleton, 1995; McAlister, 1995; Økland, 2000; Økland and Økland, 1996). Nonetheless, competition has been reported at the juvenile stage, mainly for space (Marino, 1991), light (Van der Hoeven et al., 1998) and nutrients (Twenhöven, 1992) (but see (Michel et al., 2012; Mulligan and Gignac, 2002)). Although bryophytes can inhibit another species growth, including by secreting substances that prevent the growth of protonema (Whitehead et al., 2018), competitive exclusion seems to be a rare process (Lovett-Doust and Lovett-Doust, 1988; Mälson and Rydin, 2009; Udd et al., 2016). In contrast, facilitation has been recurrently reported, allowing mosses to grow in climatically-non-suitable areas for them (Udd et al., 2016). In particular, growth in multi-specific dense cushions enhances water retention by capillarity, which increases the time period during which shoots are physiologically active (Bergamini et al., 2001; Ingerpuu and Vellak, 2013; Vanderpoorten and Goffinet, 2010; Zamfir and Goldberg, 2000).

As bryophytes grow slowly and their fitness is difficult to characterize, the use of statistical methods to study biotic interactions seems very appropriate. Preliminary results using co-occurrence analyses based on the protocol developed by D'Amen et al. (2017) were described in Collart (2018). These results showed that facilitation is an important driver for bryophyte communities and similar levels of competition as in angiosperms were observed (Collart, 2018). However, this method has been criticized for overestimating biotic interactions as available environmental data rarely allow to fully characterize species niches, so that some associations can be misinterpreted as biotic interactions (Blanchet et al., 2020). Nevertheless, careful interpretation of the results could provide baseline information on the maximum levels of biotic interactions that could take place in bryophyte communities (Blanchet et al., 2020; Dormann et al., 2018; König et al., 2021; Mod et al., 2020).

6.2.1 How to account for biotic interactions in SDMs?

Biotic interactions are usually ignored in species distribution models (Kissling et al., 2012; Wisz et al., 2013). However, it has been shown that including these interactions into SDMs allows to increase the predictive power (Anderson et al., 2002; Araújo and Luoto, 2007; Barbaro et al., 2019; Fern et al., 2019; Hof et al., 2012; Meier et al., 2011). Indeed, not including these interactions can impede the predictive capacity of SDMs to infer current and future distributions (Leathwick and Austin, 2001; Meier et al., 2010; Zurell et al., 2018, 2016). One of the first methods incorporating biotic interactions in SDMs is called joint species distribution models (JSDMs) (Pollock et al., 2014). JSDMs, which need a presence/absence matrix, compute species co-occurrences and correlate these patterns with the environment in order to obtain shared climatic niches (Ovaskainen et al., 2017, 2010; Pollock et al., 2014) and afterwards correlate the resulting residuals with species co-occurrences (Zurell et al., 2018). In theory, a positive correlation of residuals is expected if a pair of species is more often associated than expected by chance. In contrast, a negative correlation characterizes the fact that species co-occur less frequently than expected (Zurell et al., 2018). Although these residuals are usually attributed to biotic interactions, they can also coincide with other ecological mechanisms (Latimer et al., 2009; Ovaskainen et al., 2010), evolutionary processes (Pollock et al., 2015), missing environmental variables or poor model fits (Blanchet et al., 2020; Poggiato et al., 2021; Wilkinson et al., 2021; Zurell et al., 2018). Therefore, these residuals, previously interpreted in terms of biotic interactions, should be carefully interpreted as they can be for instance the result of not fully characterized abiotic niches (Blanchet et al., 2020; König et al., 2021; Zurell et al., 2018). Nonetheless, JSDMs offer new perspectives to incorporate biotic interactions as other information such as biological traits (Pollock et al., 2012) and bias corrections (Jarzyna and Jetz, 2016; Tobler et al., 2019) can easily be combined (Pollock et al., 2020). Although including biotic interactions into species distribution predictions is still challenging (Pollock et al., 2020), more and more studies try to include these interactions by various methods to more accurately predict species ranges (Barber et al., 2021; Booher and Walters, 2021; Clark et al., 2017; de la Torre Cerro and Holloway, 2021; Engelhardt et al., 2020; Golding and Purse, 2016; Harris, 2016; Maguire et al., 2016; Nieto-Lugilde et al., 2018; Staniczenko et al., 2017; Tikhonov at al., 2020; Thompson et al., 2020).

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8. Appendix – S1

Variation of Beta diversity across geographic scales and taxonomic groups in the Macaronesian land plant flora

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Introduction

Beta diversity measures the change in community composition and structural patterns along environmental, spatial and temporal gradients and has therefore appeared as a useful metric to better understand the mechanisms responsible for the variation and the maintenance of biodiversity (Soininen et al., 2018). This metric can be partitioned into two process-related components: species replacement and richness difference, which reflect two different phenomena, turnover and nestedness (Baselga, 2010). Species turnover characterizes changes in species composition along gradients of geographical and/or ecological distance (Qian et al., 2020), whereas nestedness occurs when a set of species at one site is a subset of the species at a richer site, which has typically been interpreted in terms of ordered extinction events (Baselga, 2010).

Beta diversity typically varies depending on both extrinsic (environmental) and intrinsic (biological) factors related to species niche breadth and dispersal capacities. For instance, species turnover is expected to be inversely proportional to species dispersal capacities (Soininen et al., 2018; Varzinczak et al., 2019). In land plants, this hypothesis is in line with the steeper slope of the species-area relationship reported in spermatophytes than in pteridophytes and bryophytes explained by the production of smaller, wind-dispersed diaspores in the two latter groups (Patiño et al., 2014b). Furthermore, since nestedness can only arise for areas that share a common source pool, a high nestedness at large scales is particularly expected in organisms with high dispersal capacities (Greve et al., 2005).

Beta diversity also varies depending on geographic scale (Soininen et al., 2018). If the increase of species turnover with geographic scale because of the stronger dispersal limitation and stronger environmental filtering owing to larger environmental gradients has been recurrently evidenced, (Gusmao et al., 2020; Qian et al., 2020; Soininen et al., 2018), the relationship between nestedness and geographic scale has been more controversial. Nestedness is expected to peak at a small scale if local variations of habitat quality and availability lead to variations of species richness within habitats among sites (Gusmao et al., 2020). In contrast, high nestedness at large scales is expected when extinctions vary depending on major geographic gradients (Soininen et al., 2018). This is typically the case along latitudinal diversity gradients, so that

nestedness should be greater for regions located at higher latitudes (Batista et al., 2020; Soininen et al., 2018).

Oceanic islands offer an ideal framework to investigate the variation of species turnover and nestedness across geographic scales and to determine the relative contribution of contemporary climatic factors and dispersal limitations associated to geographic isolation. Oceanic islands are in fact readily geographically circumscribed (Whittaker & Fernandez-Palacios 2007), offering naturally isolated Operational Geographic Units (OGUs). Furthermore, because they were colonized *de novo*, oceanic islands accumulate species from continental or alternative insular sources at rates depending on connectivity (distance, wind/marine currents), and endemic speciation at rates that vary with geographic isolation and species dispersal capacities (Heaney, 2000).

Here, we analyze patterns of beta diversity among the four main lineages of land plants, namely mosses, liverworts, pteridophytes, and spermatophytes, across the three northern archipelagos of the Macaronesian region (the Azores, Madeira, and Canary Islands). These archipelagos vary in terms of geographic isolation and macroclimatic conditions, so that their floras exhibit sharply different distribution patterns. In the Canarian spermatophyte flora, single-island endemics are much more frequent than multiple-island endemics, whereas the reverse pattern prevails in the Azores (Carine and Schaefer, 2010). This, together with the sharper ecological gradients in the Canaries, has led to the idea that speciation in the Canaries is primarily driven by ecological radiations, whereas allopatric diversification would prevail in Azores among islands that are more distant among each other and from continental sources than in the Canaries (Carine and Schaefer, 2010; Price et al., 2018). Spore-producing plants exhibit a lower proportion of single-island endemic and a higher proportion of Macaronesian regional endemics (i.e., taxa that are endemic to the Macaronesian archipelagos but distributed across two or more archipelagos) than spermatophytes (Vanderpoorten et al., 2011), owing to their higher dispersal capacities and allopatric speciation modes (Patiño et al., 2014a). Therefore, biogeographic relationships across Macaronesia vary among land plant lineages. Islands primarily group by archipelago despite differences in size and elevation in spermatophytes (de Nicolás et al., 1989a), whereas floristic analyses at the archipelago level revealed conflicting relationships among spore-producing floras (Vanderpoorten et al., 2007).

While spatial patterns of species richness and their drivers have already been investigated in oceanic island land plants in general (Batista et al., 2020; Patiño et al., 2013a) and in Macaronesian bryophytes in particular (Aranda et al., 2014), no study of beta diversity in land plants, and how its components vary across spatial scales and taxa, has been conducted to date in Macaronesia. In this framework, the goal of the present paper is to address the following questions and test the following hypotheses:

1 *How does beta diversity vary across taxa and archipelagos?* Given the geographic and environmental gradients observed, we expect that species turnover increases from intra- to inter archipelago comparisons (H1a). Given the higher proportion of shared species among archipelagos in spore-producing lineages, we expect this increase to be significantly lower for the latter than for spermatophytes (H1b). Finally, because of the lower environmental heterogeneity and proportion of single-island endemics in the Azores than in the Canaries, we expect that species turnover is significantly higher in the latter than in the former (H1c). We further tested the hypothesis that nestedness increases from intra- to inter archipelago comparisons (H2a). Due to the higher dispersal capacities, and hence, proportion of shared species across archipelagos in spore-producing lineages, we expect that this decrease is sharper for seed plants than for pteridophytes,

and then for mosses and liverworts (H2b) as among spore producing plants, pteridophyte produce bigger spores (30-50µm) than bryophytes (10-20µm). Finally, because variations in species richness among islands is higher in Madeira than in the Canary Islands, and then, the Azores (ref: TableS1), we expected that nestedness follows the same pattern (H2c).

2 *What are the drivers of the observed differences in beta diversity among taxa and archipelagos?*

3 *How do biogeographic affinities among islands and archipelagos vary among land plants?* Following De Nicolas *et al.* (1989), we expect that islands primarily cluster by archipelago in spermatophytes, but not in spore-producing plants, wherein islands are expected to cluster depending on climatic similarity, irrespective of the archipelago in which they are found (H3).

Material & Methods

Study area

Macaronesia (Figure 1) is a biogeographic region located in the Atlantic Ocean between 15.8 and 40.8° N (A. Hansen & P. Sunding, 1993). As the circumscription of Macaronesia has been challenged, we focused here on the Azores, Madeira (including Madeira, Porto Santos, and the Desertas islands) and the Canary Islands archipelagos. We excluded Cabo Verde, whose cryptogamic flora clearly belongs to sub-Saharan Africa (Carine, 2005; Vanderpoorten et al., 2007), and the Selvagems, whose volcanic origin is different from that of Madeira (Quartau et al., 2018; Schwarz et al., 2005), but whose very limited flora and number of islands did not warrant inclusion in the present analyses.

Data collection and matrices

Lists of moss, liverwort, pteridophyte, and spermatophyte species per island were retrieved from a review of the most recent checklists (Table S1). Due to the very low number of hornwort species (6), the latter were included within the liverworts, to which they are the most similar in terms of morpho-anatomy and life-history traits. Nomenclature follows Hodgetts et al. (2020) for mosses and liverworts, xx for pteridophytes, and xx for spermatophytes. Introduced species were excluded from the analysis as they lead, at the geographic scale of entire islands, to substantial homogenization of their floras (Otto et al., 2020).
Altogether, the data matrices included 225 liverworts & hornworts, 508 mosses, 84 pteridophytes, and 1712 spermatophytes species. These data were employed to compute, for each of the four lineages considered, species turnover (Sorensen index, βsim) and nestedness (βsne) among all possible pairs of islands using the package betapart (Baselga et al., 2018) in R version 3.6.3 (R Core Team, 2020).
Environmental variables included climatic conditions, geographic distance among islands, area, elevation, and age. The first four variables were recorded from Weigelt, Jetz and Kreft (2013). Islands age was derived from references included in Table S1. These data served to compute matrices of environmental differences among islands. The geographical distance matrix was obtained on the basis of the distance between the geographical coordinates (longitude and latitude) of each island, using the package raster (Hijmans, 2020). For climatic factors, variation in four variables reflecting the average and variation of temperature and precipitation (annual mean temperature, minimum annual temperature range, annual precipitation and variation in monthly precipitation) was summarized by a principal components analysis (PCA), the first three axes of which explained 99.6% of the variation. The Euclidian distance matrix for climatic among islands was finally computed, using the score of each island on the PCA axes as variables. Matrices of elevation, area and age distances were obtained similarly using Euclidian distance between islands.

Data analysis

Comparing turnover (βsim) and nestedness (βsne) among islands within and among archipelagos (H1a, H2a, Figure 1) involves the inclusion of the same observations multiple times (the same occurrence of a species on an island serving to compute βsim and βsne both within and among archipelagos), violating the assumption that the observations are independent from each other. We therefore computed, for each island, the average βsim and βsne values with all the other islands from the same archipelago (βintra, Figure 1). We obtained values of the average Beta diversity (βintra) between each island and all other islands of the same archipelago. Then, we computed, for each island, the average βsim and βsne values with each islands from the other archipelagos considered (βinter, Figure 1). We obtained a distribution of the average (βinter) between each island and all other islands of the other archipelagos. This distribution of average Beta values within archipelagos was then compared to that among archipelagos. Since these distributions significantly departed from normality (Kolmogorov–Smirnov test, $p<0.001$ for all lineages), were heteroscedastic (Bartlett's test, $p<0.001$ for all lineages), we applied a paired Wilcoxon rank test. Each pair was the average β between an island and all the other islands from the same archipelago on the one hand, and islands from other archipelagos on the other.

To test the increases of β from intra- to inter-archipelago (H1b and H2b, Figure 1), we computed, for each island, the difference (Δβ) of the average β between that island and all other islands from different archipelagos (βinter) and the average beta between that island and all other islands from the same archipelago (βintra) (Figure 1). The Δβ of each island were compared between lineages using a paired test where the pairs were the islands (Figure 1). Δβ values per islands for lineages were not normally distributed in the case of turnover for spermatophytes, and in the case of nestedness, for mosses, ferns, and spermatophytes. Therefore, non-parametric Friedman's and posthoc Nemenyi tests were implemented with the package PMCMRplus (Pohlert, 2021) to search for significant differences of Δβ values per island among lineages.

In order to assess, for each lineage, differences of nestedness and turnover among archipelagos (H1c and H2c), we implemented Kruskal-Wallis and posthoc Dunn tests, applying Bonferrini correction for multiple comparisons, with the package PMCMRplus (Pohlert, 2021).

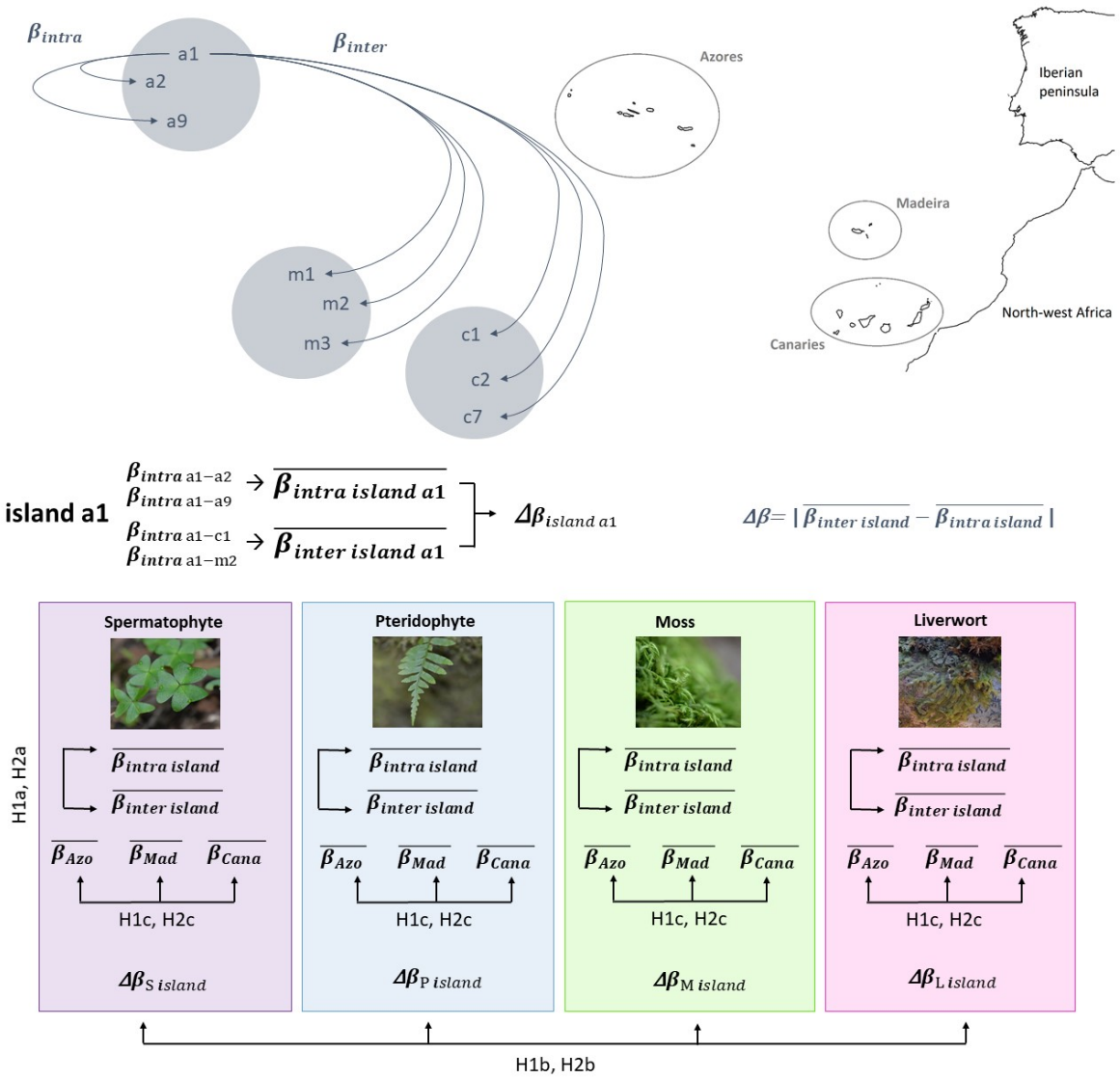

Figure 1 Study area and statistical framework to calculate Beta diversity (*β*) and its two components (βsim and βsne) between islands within (intra) and between (inter) archipelagos (the Azores Azo, the Canaries Cana and Madeira Mad) among land plants (spermatophytes S, pteridophytes P, mosses M and liverworts L).

To determine how beta diversity varies depending on geographic distance and variation in climatic conditions, age, area, and elevation across taxa and archipelagos, linear mixed-effects models (LMMs) were employed using the lme4 package (Bates et al., 2015). Fixed factors included geographic distance and variation in climatic conditions, age, area, and elevation. Random factors included 'taxon' and 'archipelago'. To facilitate the interpretation, analyses were run separately for each of the fixed effects. We first contrasted the performance of competing models including all the possible combinations of varying intercepts and slopes for the random factors considered using the Akaike information criterion corrected for small sample size (AICc), and selected the best-fit model with the step function from the lmerTest package (Kuznetsova et al., 2017). We computed an r^2 from the residual sums of squares between observed and fitted values, and compared the deviance of the LMM with the deviance of a linear intercept-only model (Kvalseth, 1985).

To address hypothesis H3, a cluster analysis of islands as a function of their taxonomic composition was performed using the Ward's method based on a total beta diversity matrix derived from Sorensen distances. The optimal number of clusters for each lineage was determined with the NbClust package (Charrad et al., 2014) using the ward cluster algorithm (Murtagh & Legendre, 2014). To help visualizing the groupings, a multidimensional scaling (MDS) based on the Sorensen distance matrix was performed.

Results

For all lineages, paired Wilcox tests showed a significant increase of turnover, but not nestedness, from intra to inter-archipelago levels (Table 1).

Table 1 Median value of turnover (βsim) and nestedness (βsne) among islands from the same archipelago (intra) and among islands from different archipelagos (inter) across land plants in Macaronesia, and p-value of the average difference between intra- and inter-archipelago comparisons (paired Wilcox test).

	Intra	Inter	p-value
		Bsim	
Spermatophytes	0.122	0.759	<0.001
Pteridophytes	0.058	0.425	<0.001
Liverworts	0.095	0.381	<0.001
Mosses	0.158	0.419	<0.001
		Bsne	
Spermatophytes	0.097	0.137	0.084
Pteridophytes	0.153	0.157	0.791
Liverworts	0.222	0.150	1
Mosses	0.213	0.192	0.802

The difference in turnover (Δβsim) between intra- and inter-archipelago comparsions is significantly higher for spore-producing plants than spermatophytes (0.58 ± 0.11) (Friedman test, p-value = 0.024), but significant differences in Δβsim for mosses (0.25 ± 0.08), liverworts (0.28 ± 0.08) and pteridophytes (0.33 ± 0.08) do not differ significantly (Figure 2, see Table S2 for exact p-values of the posthoc Friedman Nemenyi tests).

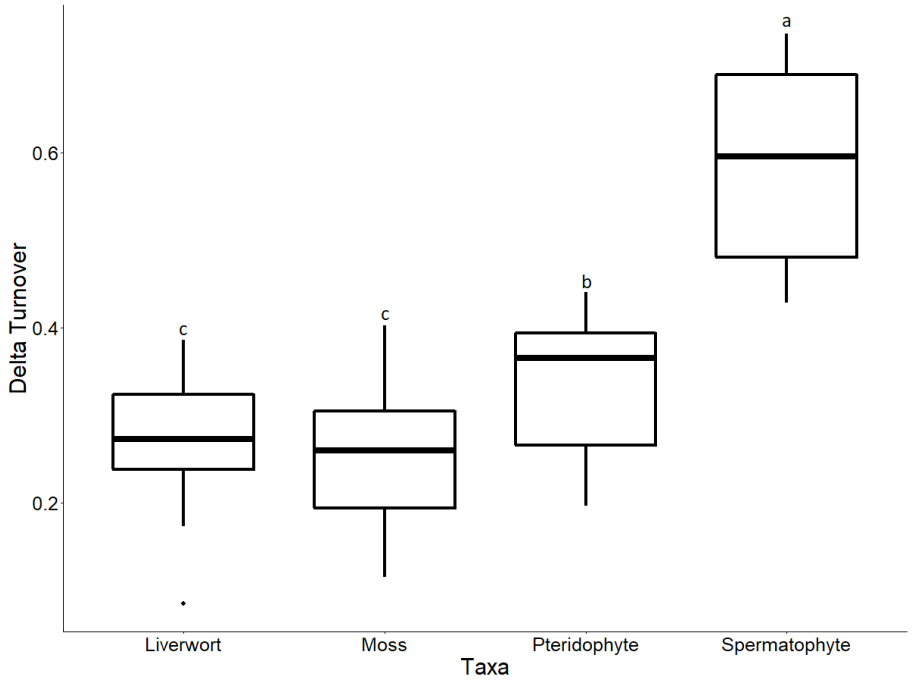

Figure 2 Box-plots (showing the 1st and 3rd quartiles (upper and lower bounds), 2nd quartile (centre), 1.5* interquartile range (edges of the box)) of the difference of turnover (Δβsim) between inter- and intra-archipelago comparisons in liverworts, mosses, pteridophytes and spermatophytes of Macaronesia. Letters above each box-plot indicate which comparisons significantly differ, identical letters being used for lineages whose turnover or nestedness does not significantly differ from each other.

The turnover among islands within archipelagos did not significantly vary among archipelagos for mosses and liverworts (Figure 3a). Conversely, turnover was significantly higher in the Canary Islands than in the Azores and Madeira in pteridophytes and, only in the Azores for spermatophytes (see Table S3 for exact p-values of the Kruskal-Wallis tests). Nestedness among islands within archipelagos did not significantly vary among archipelagos for mosses and liverworts (Figure 3b). In pteridophytes and spermatophytes, conversely, nestedness was significantly higher in Madeira than in Azores, but similar in the Canaries (see Table S4 for exact p-values of the Kruskal-Wallis tests).

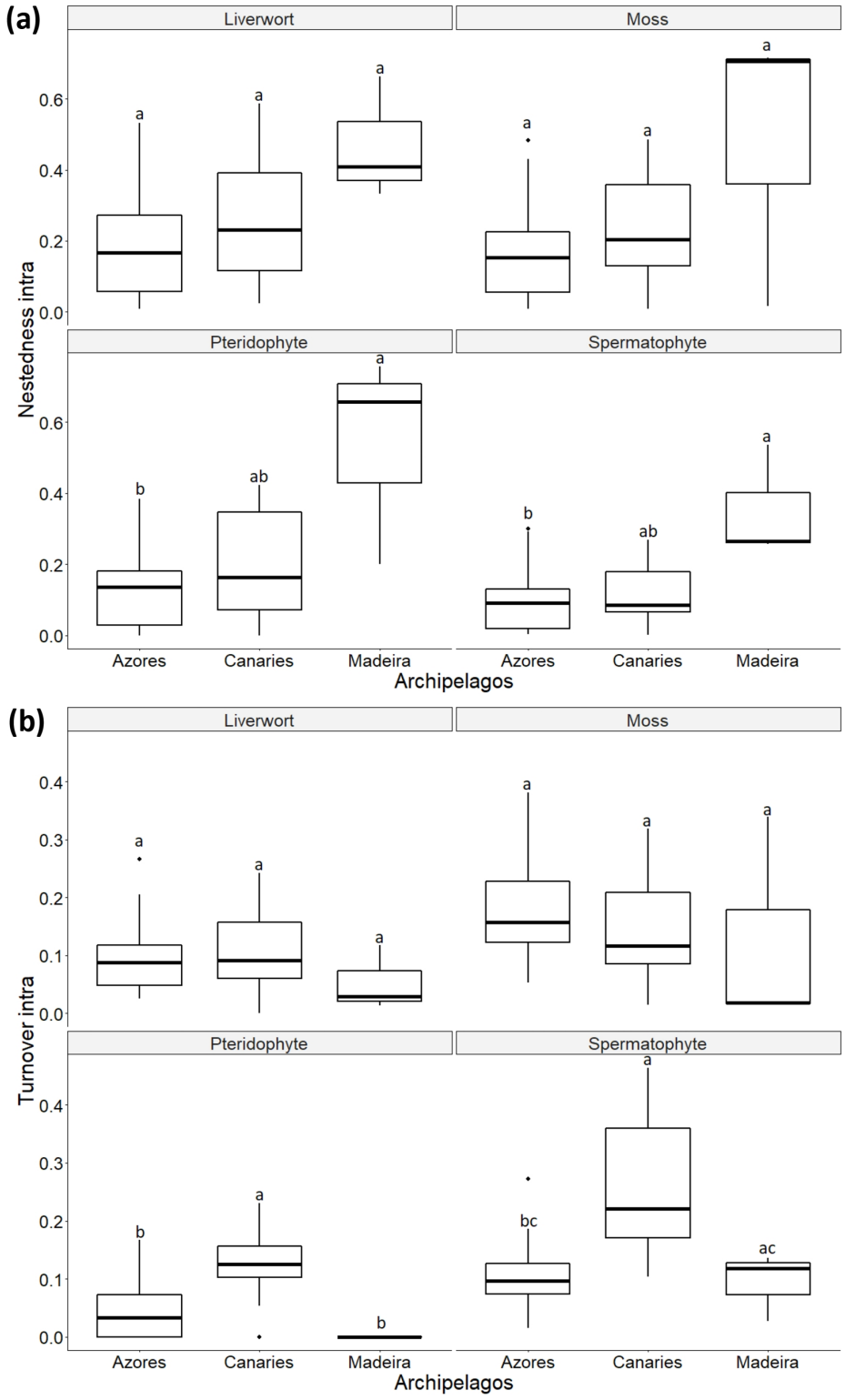

Figure 3 Box-plots (showing the 1st and 3rd quartiles (upper and lower bounds), 2nd quartile (centre), 1.5* interquartile range (edges of the box)) of (a) turnover and (b) nestedness among islands from the same archipelago in liverworts, mosses, pteridophytes and spermatophytes of Macaronesia. Letters indicate, for each lineage, the archipelagos among which turnover significantly differs, with the same letter indicating non-significantly different average values between the archipelagos considered.

The model selected for turnover as a function of climatic variation while controlling for the factors 'taxon' and 'archipelago' included a random intercept for 'taxon' and 'archipelago' and a non-correlated random slope for 'archipelago', but not 'taxon'. Model r^2 was 0.43. Turnover increased with climatic variation, except in Madeira, with steeper slopes in Azores than in the Canary Islands (Figure 4a).

Regarding geographic distance, the best-fit model of turnover included a random intercept for 'taxon' and for 'archipelago'. Model r^2 was 0.39. The slopes were positive and did not vary among archipelago nor among taxa (Figure 4b). In contrast, a random slope for 'taxon' and 'archipelago' was included in the selected models for difference in area, elevation and age between island, respectively (Fig. 4c-e). Model r2 were 0.38, 0.47 and 0.44, respectively. The turnover of all lineages positively varied with differences in elevation, with steeper slopes in spermatophytes and mosses than in pteridophytes and liverworts, and in the Canary Islands than the Azores (Fig. 4c). For the factors age and area, the slopes for mosses and liverworts were negative, but positive for pteridophytes and spermatophytes (Fig. 4d-e).

For nestedness, the best-fit models for all fixed factors included a random intercept for 'taxon' (plus 'archipelago in the case of geographic distance) and a random slope for 'archipelago'. Model r2 ranged between 0.31 and 0.48 (Fig. S5). Nestedness was negatively correlated with climatic variation, geographic distance, difference of elevation in the Azores, whereas the reverse tend was observed in Madeira and the Canaries (Fig. S5a-c). For age difference, the slopes were positive in the Azores and the Canaries, but negative in Madeira (Fig. S5d). Finally, nestedness did almost not vary with area in the Azores and the Canaries, whereas a sharp increase of nestedness with area was observed in Madeira (Fig. S5e).

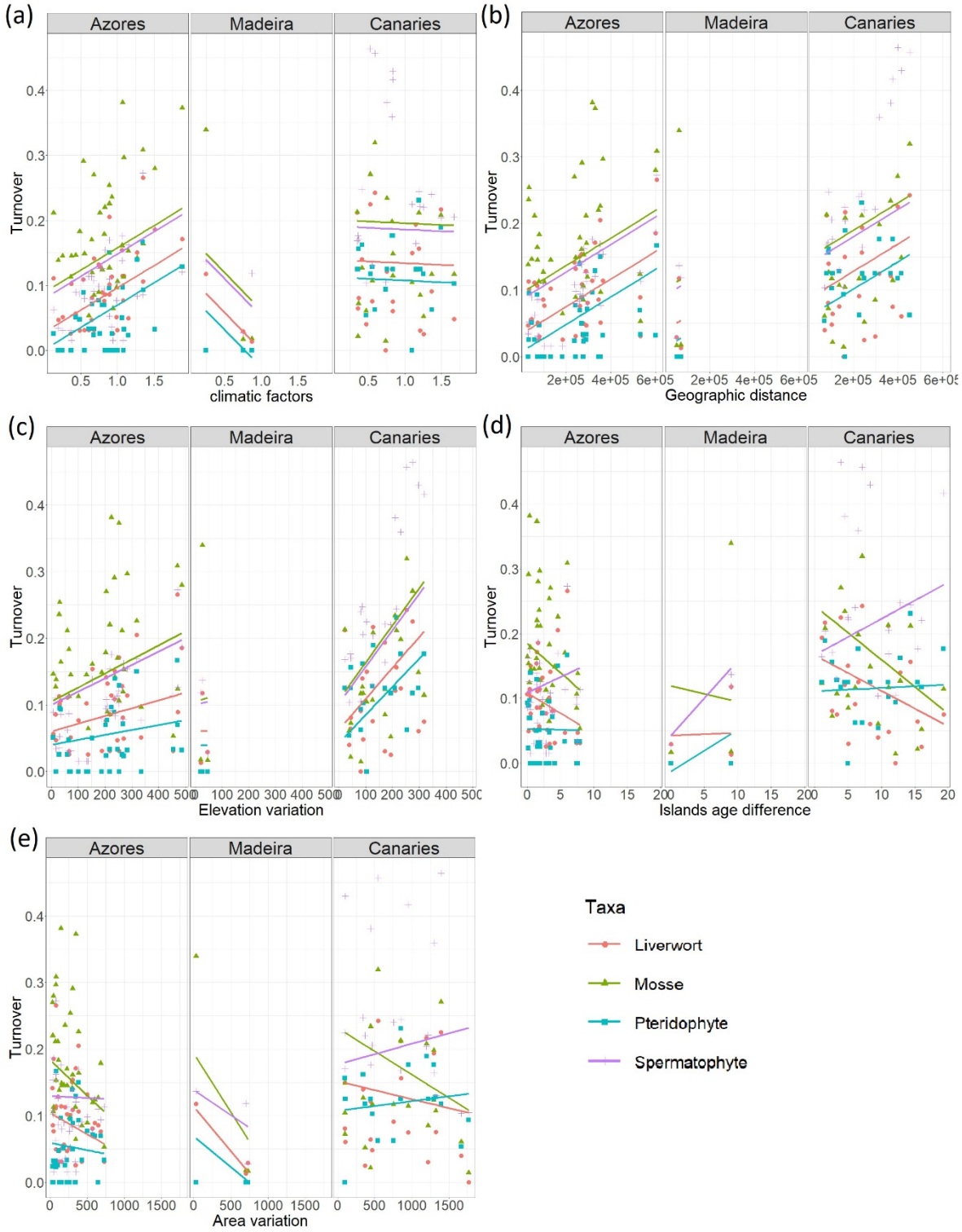

Figure 4 Linear mixed-effect models describing variation of turnover among spermatophyte, pteridophyte, liverwort and moss floras in the Canary Islands, the Azores and Madeira depending on climatic variations (a) geographic distances (b), elevation variation (c), age difference (d) and area variation (e) in Macaronesia while controlling for differences among taxa and archipelagos.

The results of the clustering analyses grouping islands as a function of their species composition in each lineage are shown in Figure 5. In spermatophytes, the three clusters identified correspond to the Azores, the Canary Islands and Madeira. In liverworts, the Azorean islands clustered together, the Canarian islands of Fuerteventura and Lanzarote, and the Desertas of Madeira archipelago, formed a second cluster; while Madeira clustered with Porto Santos and the remaining Canary Islands. The grouping observed with the moss floras was almost identical, except that Porto Santos clustered with Fuerteventura and Lanzarote, and the Desertas. In pteridophytes, Madeira clustered with the Azores; Porto Santo and, Desertas (Madeira archipelago), Lanzarote and Fuerteventura (Canary Islands) formed a second cluster; and the western Canary Islands formed the third cluster.

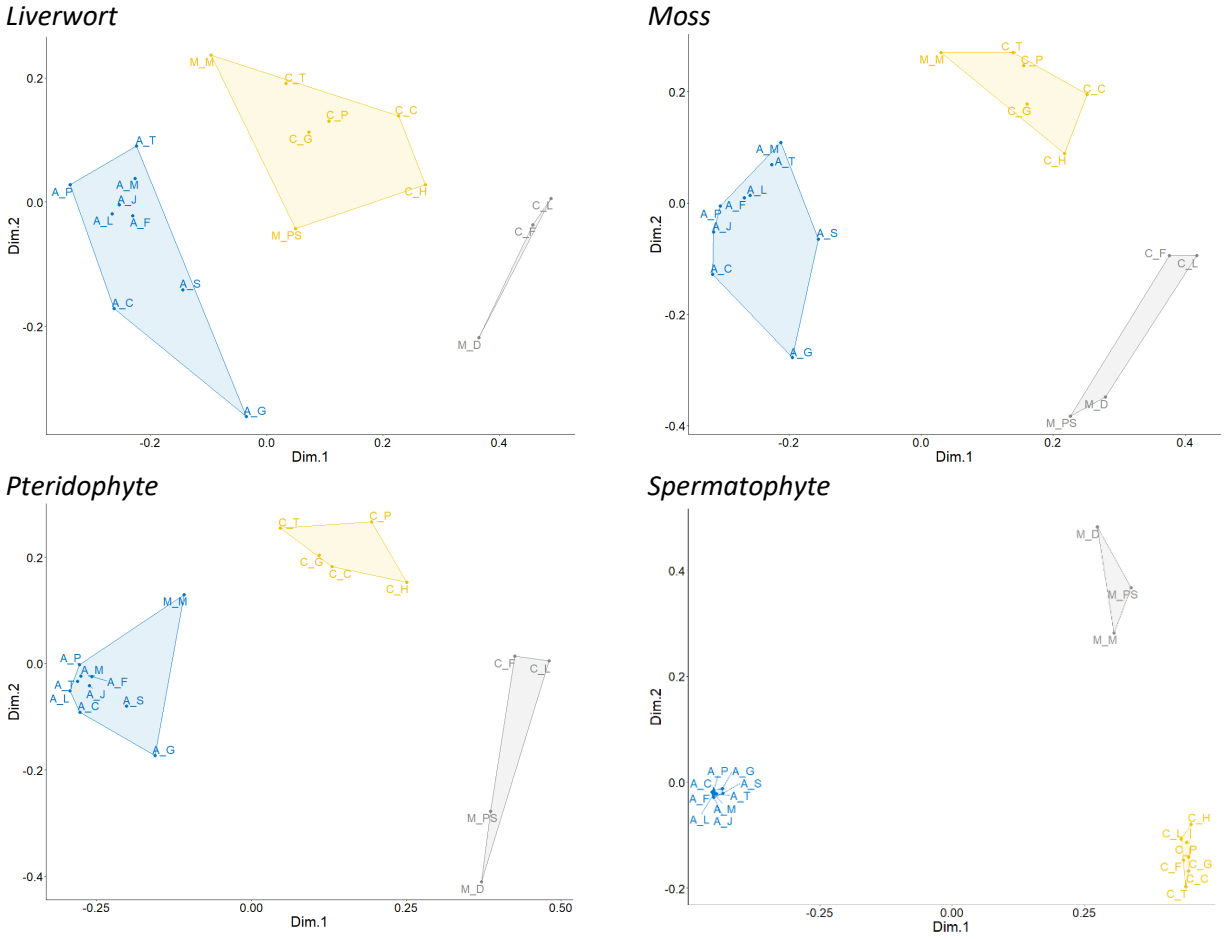

Figure 5 NMDS ordination of the Macaronesian islands depending on their floristic composition (spermatophytes, pteridophytes, mosses and liverworts), based on Sorensen matrix. Colours represent the clusters identified using Ward's clustering algorithm and defining the optimal number of clusters using NbClust.

Discussion

Our analyses on the spatial patterns of variation of beta diversity and its components across land plants in Macaronesia revealed that turnover, but not nestedness, significantly increased from intra- to inter-archipelago comparisons. The increase of turnover with the extent of the geographic scale is in line with our hypothesis H1a. Based on theoretical and empirical evidence pointing to the role of stronger dispersal

limitation and environmental filtering owing to longer environmental gradients and larger geographic distances across larger scales (Menegotto et al., 2019; Soininen et al., 2018, 2007).

The extent of this increase varied, however, among lineages, being larger in spermatophytes than in pteridophytes, and then, mosses and liverworts, wherein the median turnover was less than half that in spermatophytes. In contrast with this finding, the slope of the species-area relationship, which reflects the beta diversity among communities (Triantis et al., 2012), did not significantly vary among land plant lineages across Macaronesia (Aranda et al., 2014), these sharp differences are in line with our expectations (H1b), that the progressive decrease of turnover from spermatophytes to bryophytes reflects their dispersal capacities and distribution patterns. Thus, endemic spermatophyte species, which represent about 40% of species richness, tend to occur one single islands (Carine and Schaefer, 2010). In Macaronesian pteridophytes and bryophytes in contrast, island endemism is of a few percents, single island endemic bryophyte and pteridophyte species are almost inexistent (Patiño et al., 2013b), and species tend to be widely distributed across islands, as illustrated by skewed presence per k islands curves (Vanderpoorten et al., 2011).

In contrast with the idea that variation of turnover typically results from environmental filters and dispersal limitations (Tsiftsis, 2020, Liu et al., 2020), differences of turnover among land plant lineages could not be attributed to differences in response to climatic variation or geographic distance among lineages. In fact, a random slope for the factor 'taxon' was not included in the selected model linking turnover and these factors, suggesting that all lineages responded similarly to them. In spermatophytes, a positive relationship between turnover and geographic distance was evidenced, including in lineages with small seeds such as orchids (Tsiftsis, 2020), but this pattern was unexpected in bryophytes, wherein similar values of turnover were actually observed among island communities and those expected under a null model, according to which species can randomly disperse among islands (Liu et al., 2020). While the positive relationship observed here between bryophyte turnover and geographic distance may reflect a correlation between geographic distance among Macaronesian islands and other factors of island age and elevation (see below), it is worth noting that isolation-by-distance slopes derived from analyses of spatial genetic structures in bryophytes range within the values reported for spermatophytes (Ledent et al., 2020; Vanderpoorten et al., 2019), despite the much larger diaspores of the latter, evidencing dispersal limitations.

Different responses of turnover among lineages were observed with regard to elevation, but with steeper slopes in mosses and spermatophytes than in liverworts and ferns, and thus not accounting for the higher turnover in spermatophytes than in bryophytes. The steeper slopes between turnover and elevation observed for mosses as compared to liverworts and ferns suggest that there are more elevation-specialists along the entire elevation gradient in the former than in the latter. In the Canary Islands, liverworts in fact exhibit a peak of species richness at 1000m and are virtually missing above 1600m, whereas species richness is more evenly distributed, including towards the highest elevations, in mosses (Hernández-Hernández et al., 2017).

Lineage-specific differences of turnover were also observed with regard to island age and area. While species turnover was positively correlated with variation of these factors in spermatophytes, the reverse trend was observed in mosses and liverworts. In fact, the bulk of the endemic element in the Macaronesian bryophyte flora is, in contrast to the spermatophyte flora, restricted to the laurel forest (Patiño et al., 2014b). This element is largely absent from the oldest islands, such as Fuerteventura and Lanzarote in the Canary Islands, whose xerophytic, lowland flora is largely shared with that of the low-elevation areas found on younger islands. As a result, there are more floristic differences among the laurel forest floras of

relatively young islands than between a young and an old island, whose shared lowland element results in the observed increase of nestedness with island age.

In agreement with our hypothesis H1c, patterns of turnover also varied among archipelagos in pteridophytes and spermatophytes, but not in bryophytes. The highest turnover observed in the Canaries for spermatophytes and pteridophytes, despite the shorter distance between islands than in Azores, reflects the steeper altitudinal floristic gradients, as best illustrated by the steeper regression slopes between turnover and elevation in the former archipelago than in the latter, as well as, globally, greater heterogeneity in climate, islands age and habitats between the Canarian islands than the Azorean islands (del Arco Aguilar M.J., 2018; Triantis et al., 2012). These differences are well reflected in the distribution of endemism among archipelagos, with the bulk of Canarian endemics being single-island endemics, whereas Azorean endemics tend to be multiple-island endemics, widespread across the archipelago (Carine and Schaefer, 2010). The similarity of turnover among archipelagos in bryophyte floras is, at first sight, more striking. In fact, bryophytes are poikilohydric, and large differences in species composition would be expected between the eastern Canary Islands (Fuerteventura and Lanzarote), which are characterized by low elevation and dry climates, and the western Canary Islands, with higher elevation and wetter climates. In reality, the specialized xerophytic floras of the eastern Canary Islands, dominated by thalloid liverworts (*Riccia spp.*) and annual mosses (especially of the family Funariaceae), can also be found at low elevation on South-facing slopes of the western Canary Islands. As a result, Canarian bryophyte communities are more nested than Canarian spermatophyte communities, and these nestedness patterns are indeed highly correlated with climatic variation, as evidenced by the steep slopes of the regression between nestedness and climatic variation.

Contrary to our hypothesis H2a that nestedness will increase with scale (see Soininen *et al.*, 2018 for reviews, but see Menegotto *et al.*, 2019), there was no difference of nestedness between intra- and inter-archipelago comparisons. Nestedness arises when species-poor sites represent subsets of the biota occurring in species-rich sites (Baselga, 2010; Cantor et al., 2017). In Macaronesian bryophytes, pteridophytes and spermatophytes, species richness patterns are similar across archipelagos, so that no clear nested pattern is apparent. Differences in species richness among archipelagos are more evident in spermatophytes, with 1066, 373 and 127 native species in the Canarian, Madeiran and Azorean floras, which is reflected by the near-significance of the difference of nestedness in intra vs among archipelago comparisons in spermatophytes.

There were, however, significant differences of nestedness among archipelagos in the spermatophyte and pteridophyte floras, with a recurrent pattern across taxa according to which nestedness in Madeira was significantly higher than in other archipelagos. Nestedness in bryophytes exhibited the same pattern, albeit not significant. The archipelago of Madeira was represented in our analyses by Madeira, Porto Santos and the Desertas archipelago. The latter two exhibit much lower elevation, and much drier climates than Madeira, so that their species richness is comprised of the most drought-tolerant elements of the Madeiran flora, resulting in a strong nested pattern that correlates with variation in climatic conditions.

As a result of the relevance of climatic filters and the much greater importance of geographic isolation to explain beta diversity patterns in spermatophytes than in pteridophytes and bryophytes, spermatophyte floras clustered by archipelago, as expected (H3) and as previously evidenced (de Nicolás et al., 1989b) whereas pteridophyte and bryophyte floras did not. In the absence of significance of geographic isolation to explain beta diversity in the latter, island floras cluster depending on macroclimatic similarities, regardless of the archipelago structure. Therefore, Fuerteventura, Lanzarote, Desertas and Porto Santo host similar

cryptogrammic floras of low-elevation, dry islands, whereas the western Canary Islands and Madeira, which share typical laurel forest floras, form another cluster. The closer similarity of the Canarian and Madeiran floras in bryophytes, which is at odds with previous analyses at the archipelago level (Vanderpoorten et al., 2007), contrasts with the closer similarities between the Azorean and Madeiran pteridophyte floras.
The present study shows that the dispersive capacities of land plants as well as the climatic conditions between the islands do not fully explain the differences in distribution between the Macaronesian flora lineages. Indeed, the factor 'taxon' was never link to neither 'climatic variation', 'geographical distance' nor any other abiotic factors in the LMM. In addition, significant differences are observed within the spore-producing plants, notably in the turnover pattern between pteridophyte and bryophyte. These differences in the similarities among land plant lineages in the Macaronesian flora suggest that different mechanisms explain the assembly of these floras and call for a comparative analysis of the geographic origin of these floras in an explicit time-frame. Studying beta diversity at an even finer scale, such as the level of biomes within each island as a control for habitat heterogeneity based on elevation variable, would also be promising for identifying potential links between the continental origins of the Macaronesian flora population and thus clarify the mechanisms of diversification and colonization among the different land plant lineages.

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Appendix

Table S2 Origin and references of the lists of presence of flora (Bryophytes, Pteridophytes and Spermatophytes) per island from three Macaronesian archipelagos (Azores, Canaries and Madeira) and references used to date 19 Macaronesian islands.

Bryophytes from the Madeira islands	Bryophytes from the Canary Islands
Ellis, L. T. *et al.* (2014) 'New national and regional bryophyte records, 40', *Journal of Bryology*, 36(3), pp. 223–244. doi: 10.1179/1743282014Y.0000000115.	Dirkse, G. M. *et al.* (2018) 'New bryophyte records from Macaronesia', *Cryptogamie, Bryologie*, 39(1), pp. 61–76. doi: 10.7872/cryb/v39.iss1.2018.61.
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Bryophytes and Spermatophytes from the Azores islands	**Spermatophytes from the Canaries islands**
Borges, P. A. V. *et al.* (2010) *Listagem dos organismos terrestres e marinhos dos açores - A List of the terrestriaL and marine biota from the azores*, *Biologia*.	Work in progress
Spermatophytes from the Madeira islands	**Pteridophytes**
Work in progress	Work in progress

Island ages

Azevedo, J. M. M. and Portugal Ferreira, M. R. (1999) 'Volcanic gaps and subaerial records of palaeo-sea-levels on Flores Island (Azores): Tectonic and morphological implications', *Journal of Geodynamics*, 28(2–3), pp. 117–129. doi: 10.1016/S0264-3707(98)00032-5.

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Table S2 P-values, with Bonferronni correction, resulting from the Friedman posthoc test for comparing inter-intra difference (the mean difference between turnover of islands from different archipelagos and turnover of islands from the same archipelago of each island) among four plant taxa (Spermatophyte, Pteridophyte, Liverwort and Moss) in Macaronesia.

	Pteridophytes	Liverworts	Mosses
Seed plants	0.004	7.8e-07	9.4e-08
Pteridophytes	-	0.235	0.107
Liverworts	-	-	0.982

Table S3 Mean (±S.D.) of the turnovers of islands from the same archipelago and p-value, adjusted with Bonferronni, from of the Kruskal-Wallis tests on intra turnover among three Macaronesian archipelagos (Azores, Canaries and Madeira) for four land plant taxa (Spermatophyte, Pteridophyte, Liverwort and Mosse).

	Azores	Canaries	Madeira	p-value
Spermatophytes	0.100 ± 0.055	0.254 ± 0.115	0.094 ± 0.059	$6.970\ 10^{-7}$
Pteridophytes	0.047 ± 0.048	0.123 ± 0.052	0 ± 0	$7.980\ 10^{-6}$
Mosses	0.181 ± 0.083	0.139 ± 0.081	0.125 ± 0.186	0.115
Liverworts	0.095 ± 0.056	0.113 ± 0.073	0.053 ± 0.056	0.268

Table S4 Mean (±S.D.) of the nestedness of islands from the same archipelago and p-value, adjusted with Bonferronni, from of the Kruskal-Wallis tests on intra nestedness among three Macaronesian archipelagos (Azores, Canaries and Madeira) for four land plant taxa (Spermatophyte, Pteridophyte, Liverwort and Mosse).

	Azores	Canaries	Madeira	p-value
Spermatophytes	0.100 ± 0.092	0.113 ± 0.082	0.353 ± 0.158	0.035
Pteridophytes	0.138 ± 0.127	0.203 ± 0.155	0.538 ± 0.297	0.022
Mosses	0.161 ± 0.124	0.233 ± 0.150	0.480 ± 0.400	0.111

Liverworts	0.190 ± 0.150	0.268 ± 0.166	0.468 ± 0.174	0.026

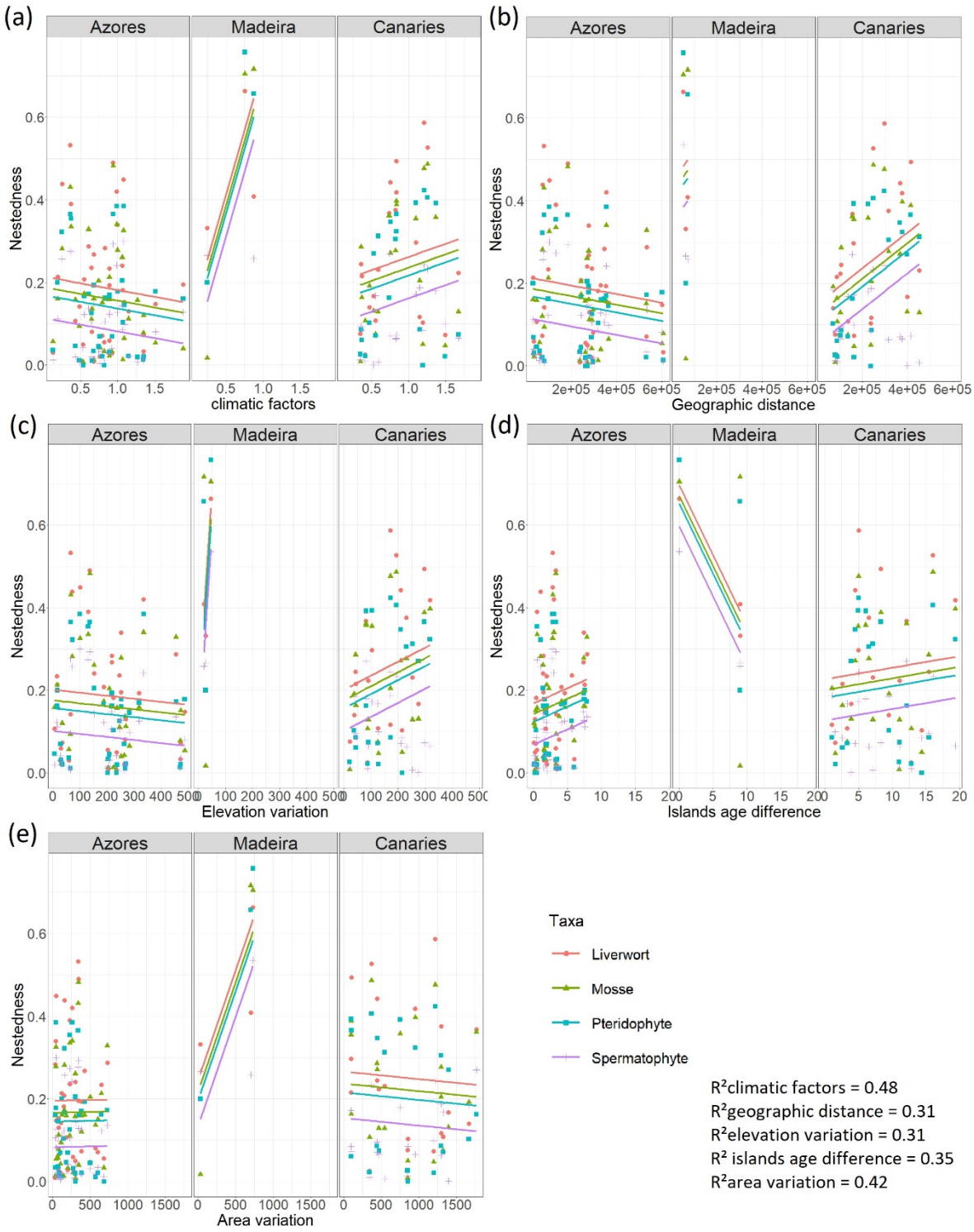

Figure S5 Linear mixed-effect models describing variation of nestedness among spermatophyte, pteridophyte, liverwort and moss floras in the Canary Islands, the Azores and Madeira depending on climatic variations (a) geographic distances (b), elevation variation (c), age difference (d) and area variation (e) in Macaronesia while controlling for differences among taxa and archipelagos.